Ecological Approaches to Managing Crop Diversity for Sustainability and Resilience in the Great Lakes Region

by

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Dedication

This dissertation is dedicated to all the teachers, mentors, and role models in my life, without whose encouragement I would have never embarked on this journey. Thank you.

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Abstract

Mounting evidence suggests that increasing crop diversity on farms improves agroecosystem sustainability and resilience, especially when increasing functional diversity, such as with non-harvested cover crops. However, crop diversification practices remain understudied in the context of working farms, where a wide range of factors interact to influence plant growth and associated benefits. Chapter 1 introduces how this dissertation integrates principles of functional, community, and ecosystem ecology to investigate outcomes of different types and levels of crop rotation diversity across the heterogeneous environmental and management conditions present on farms in the Great Lakes region.

In the first dissertation study (Chapter 2) I explore how functionally diverse cover crop species respond to a gradient of soil health and interspecific interactions when grown together in mixture. Using a trait-based approach, this two-year experiment on eight farms with distinct management histories revealed species-specific responses to soil properties. Competitive and facilitative interactions drove trait plasticity within species, and trait variation within species was as large as that between species, highlighting the need for considering both inter- and intraspecific trait variation when selecting cover crop species. Because trait variation can scale up to influence agroecosystem function, these findings demonstrate that tailoring cover crop management based on context is important for meeting sustainability goals.

In the second study (Chapter 3) I use an observational, citizen science approach to examine patterns and drivers of cover crop performance on 253 farm fields across the Great Lakes region between 2021-2023. Cover crop performance was highly variable across fields. Compared to cereal rye, the most popular cover crop in the region, mixtures accumulated twice as much biomass and nitrogen, in part because they were grown as part of more diverse crop rotations. Mixtures with high species richness performed best, suggesting that functional redundancy offers insurance across heterogeneous growing conditions. For lower diversity mixtures, use of organic soil amendments buffered against the negative effects of low precipitation. These findings demonstrate that increasing plant diversity can optimize cover crop outcomes on working farms, and highlight synergies when using multiple ecological management practices.

In the final study (Chapter 4) I use remote sensing data to test relationships between crop diversification and agroecosystem climate resilience for the lower peninsula of Michigan from 2008-2019. Results of panel fixed effects models and linear regressions indicate that adding overwintering cover crops into rotations offers significant benefits for yields and yield stability. Although heavy spring rainfall delayed primary crop planting dates, delays were reduced with each year of prior cover crop use. Importantly, the positive effects of cover crops took several years to appear, underscoring that continued, long-term use is critical for restoring ecological processes that build climate resilience.

Chapter 5 summarizes key takeaways and implications. Taken together, the three studies highlight the importance of functional diversity for supporting beneficial outcomes in agroecosystems, and that research situated within real world farming conditions is critical for identifying context-dependent relationships. The wide variation in cover crop performance, and benefits that may not be immediately apparent, suggest a need for greater technical and financial support during early stages of transitions to more diversified systems as farmers gain experience and wait for tangible benefits to accrue. In sum, results demonstrate that integrating ecological science with agricultural research is key to advancing food system sustainability and resilience.

Chapter 1 – Introduction

1.1 Agroecology

Agricultural systems science largely originated in the field of agronomy, with the principal goal of maximizing productivity. To meet this goal, agronomic research and practice has focused on how to deliver key limiting resources to crops while controlling most other factors, largely through application of external inputs like fertilizers and pesticides. However, this industrial approach to agriculture has come at a significant cost. Reducing agricultural systems to a few main components and interactions has resulted in extensive negative externalities, including soil degradation, water pollution, greenhouse gas emissions, biodiversity losses, and social inequities (Crippa et al., 2021; IPBES, 2019). This has prompted calls for a new agricultural paradigm that considers outcomes beyond yield (Matson et al., 1997; Robertson et al., 2014; Rasmussen et al., 2024).

In response, the field of agroecology has emerged as a science, practice, and social movement for transforming food systems into those that are sustainable, resilient, and just (Wezel et al., 2009). As a science, agroecology draws on ecological knowledge and concepts to study agricultural ecosystems, or "agroecosystems." This ecological thinking is then manifested as a set of management practices that foster key ecological processes and interactions on farms. Agroecology as a social movement emphasizes sovereignty and equity across all aspects of the food system. By bolstering the ecological integrity of agroecosystems and reducing reliance on external inputs, agroecology as a science and practice supports movements to shift food systems away from industrialized models to those in which social and ecological components operate in harmony (Gliessman, 2018). In this dissertation, I focus on the science and practice of agroecology in the Great Lakes region, specifically testing the application and outcomes of ecological principles in row crop systems.

1.2 Applying ecological principles to agroecosystems

The field of ecology offers a useful framework for holistic, systems-level analysis and management of agroecosystems (Lowrance et al., 1984; Swinton et al., 2007). An ecological approach to food production embraces agroecosystem complexity to better manage for multiple functions that vary over time and space (Drinkwater, 2002; Kremen & Miles, 2012). Rather than suppressing the suite of biological interactions and processes that can occur in agroecosystems, ecologically-based management harnesses those interactions and processes to create a more sustainable and resilient food system (Shennan, 2008). By mimicking the types of interactions and processes that occur in natural systems, ecological approaches to agriculture support critical ecosystem functions. For instance, natural ecosystems often maintain closed-loop nutrient cycles that enable long-term productivity with relatively small losses to surrounding ecosystems. This is in part driven by high levels of diversity. Specifically, a rich body of literature suggests that functional diversity, or the number of different species with unique traits or roles in the ecosystem, is key to maintaining ecosystem functions and services (Cadotte et al., 2011; Cardinale et al., 2011; Loreau et al., 2002).

Functionally diverse plant communities contain species with different phenological, morphological, physiological, and chemical traits (i.e., functional traits), thus exhibiting niche differentiation that increases functional diversity in both time and space. Differences in phenology allow for maintaining continuous soil cover and carbon inputs to soil, and maximizing the portion of the year in which living roots interact with soil microorganisms. This then supports soil functions – including soil carbon accrual, nutrient retention and mineralization, soil aggregation, and water infiltration and retention (Garland et al., 2021; King & Blesh, 2018; Zak et al., 1990, 2003) – that are central to sustainable and resilient agroecosystems (Lehmann et al., 2020). Co-existing species can exhibit complementarity in space that enhances overall resource-use efficiency and productivity (Cardinale et al., 2007; Loreau & Hector, 2001), such as when contrasting root morphologies allow for greater water and nutrient uptake from soil (Brooker et al., 2015).

Further, interactions among species can benefit ecosystem productivity and function (Brooker et al., 2016; Cardinale et al., 2002). Facilitation occurs when one species improves the growing conditions for another, for instance when legumes partner with their bacterial symbionts to increase total ecosystem nitrogen (N) availability through biological N fixation. This process is particularly relevant in agroecosystems, where removal of limiting nutrients in harvested crops can be offset by N inputs from legumes. Although competition can reduce species diversity, it can also be beneficial when carefully managed, such as when using fast-growing species to outcompete weeds. Importantly, the degree to which multiple ecosystem functions are supported depends on the relative representation of different species (Grime, 1998), but the performance of each species can vary significantly across growing conditions. There is thus increasing recognition that, in addition to functional trait differences between species (i.e., interspecific trait variation), functional trait variation within species (i.e., intraspecific trait variation) may be key to understanding plant responses to, and effects on, their environment (Garnier & Navas, 2012).

In sum, by strategically managing species diversity in agroecosystems, farmers can rely on ecological interactions and processes to support agroecosystem functions, and reduce reliance on environmentally and economically costly external inputs (Altieri, 1999). Although there are many ways to add diversity to an agroecosystem, this dissertation focuses specifically on crop diversity. In particular, the research presented here draws on the ecological principles outlined above to examine patterns and outcomes of crop diversification in the U.S. Great Lakes region.

1.3 Crop diversification in the Great Lakes region

Farms in the Great Lakes region produce a wide variety of food, forage, and energy crops, but also contribute to extensive environmental disservices, including greenhouse gas emissions and nutrient pollution of freshwater resources (Michalak et al., 2013; Robertson et al., 2000). At the same time, increasingly variable and extreme precipitation patterns threaten crop production and farmer livelihoods (Melillo et al., 2014). There is thus a critical need to identify strategies for improving agroecosystem sustainability and resilience. One promising approach is incorporating greater crop functional diversity (Martin & Isaac, 2015, 2018; Wood et al., 2015). Because many agroecosystems contain low levels of species diversity, there are numerous opportunities to strategically fill previously unoccupied niches.

In the Great Lakes region, agroecosystems are dominated by simplified grain rotations with winter bare fallows in between. Increasing rotation diversity (i.e., diversity of crops over time) by replacing winter fallows with species that fill the overwintering niche is a crucial opportunity for enhancing temporal functional diversity. Species that overwinter help maintain continuous living plant cover, reduce soil erosion, and minimize nutrient losses (Tonitto et al., 2006). Common crop options include small grains like winter wheat, or perennial forages like alfalfa. Increasingly, overwintering cover crops are gaining traction as a promising option for increasing agroecosystem diversity. Cover crops are non-harvested crops grown specifically to enhance ecosystem functions and services.

Overwintering cover crops increase crop functional diversity through time, but can also increase spatial functional diversity when multiple species with complementary characteristics are combined in mixtures. Mixtures allow for supporting multiple ecosystem functions at once, or multifunctionality (Blesh, 2018; Finney & Kaye, 2017; Storkey et al., 2015). For example, N fixation by legumes, fibrous roots of grasses, and taproots of brassicas can simultaneously supply N, retain N, and reduce soil compaction. At the same time, contrasting traits in mixture can drive interspecific interactions that, in turn, influence individual species performance, mixture composition, and ecosystem functions (Berg & Ellers, 2010). Cover crops may also excel at building soil organic matter (SOM) compared to harvested crops because they contribute organic inputs with both high quantity and quality to soil (King & Blesh, 2018; McDaniel et al., 2014). Resulting higher levels of SOM may build resiliency by increasing nutrient cycling, soil aggregation, water infiltration and retention, and productivity (Hudson, 1994; Kane et al., 2021; Williams et al., 2016). Overwintering cover crops may therefore aid in climate change adaptation (Kaye & Quemada, 2017).

1.4 Agroecological research on working farms

Despite the potential benefits of crop diversification practices, they remain understudied in real-world contexts. Most crop diversification research has been conducted at field stations under relatively controlled experimental conditions that do not fully capture the wide range of factors at play on working farms. Furthermore, many of the factors that influence diversification outcomes act at different spatial and temporal scales. At large spatial scales, differences in environmental conditions, such as climate and soil type, may drive outcomes across farms, while at smaller spatial scales, management regimes can interact with environmental factors to affect the success of diversification practices. Crop diversification outcomes may also change over time as agroecosystems transition to new steady states with implementation of new practices (Robertson et al., 2014; Tamburini et al., 2020), or in response to interannual variability in climatic conditions (Bowles et al., 2020). Additionally, farmers regularly adapt their management based on a dynamic and interacting set of environmental, political, social, and economic conditions (Epanchin-Niell et al., 2022). This complex suite of factors necessitates research that embraces real-world variability to better understand and predict crop diversification outcomes on working farms.

One approach is to conduct on-farm experiments in partnership with producers, which can help ensure the research is actionable, adapted to local conditions, and aligned with farmers' needs (Lacoste et al., 2022; Snapp et al., 2019). Researchers and producers collaboratively develop experimental treatments, determine outcomes of interest, and interpret results. When replicated across several farms, this approach can be ideal for identifying how management gradients and environmental conditions influence diversification outcomes. However, these experiments often involve extensive measurement and monitoring of multiple explanatory and response variables, and can thus be time and resource-intensive. This can then limit the spatial and temporal scales at which on-farm experiments are performed.

At larger spatial scales, community and citizen science approaches are gaining traction for tackling natural resource questions (McKinley et al., 2017). Citizen science engages members of the public in the research process to enable data collection across large geographic areas, such as when farmers collect and report observations of plants, soil, and insects from their fields (Ryan et al., 2018). This type of observational approach is ideal for fully situating research within the conditions and constraints of real farms, as well as capturing innovative and placed-based practices. Although it is more difficult to determine cause and effect compared to on-farm experiments, the pairing of field observations with management information reported by farmers can facilitate robust analyses. Citizen science may be limited in its ability to track farm- and field-scale temporal trends, though, because participation often changes from year to year.

Remote sensing can generate data at both large spatial and temporal scales. This can be especially useful for assessing interannual trends in agroecosystem function in response to shifting climatic patterns, and examining how adoption of crop diversification practices changes ecosystem function over time. However, remote sensing remains limited in the types of variables it can detect and accurately quantify, particularly when it comes to finer-scale management details, such as nutrient and pest management, tillage types, and seeding rates. There are therefore important benefits and tradeoffs to each of the approaches discussed above that influence the types of questions they are well-suited to address. In this dissertation, I apply these different methods to comprehensively investigate how various types and levels of crop diversity perform across the heterogeneous environmental and management conditions present on farms in the Great Lakes region (Figure 1-1).

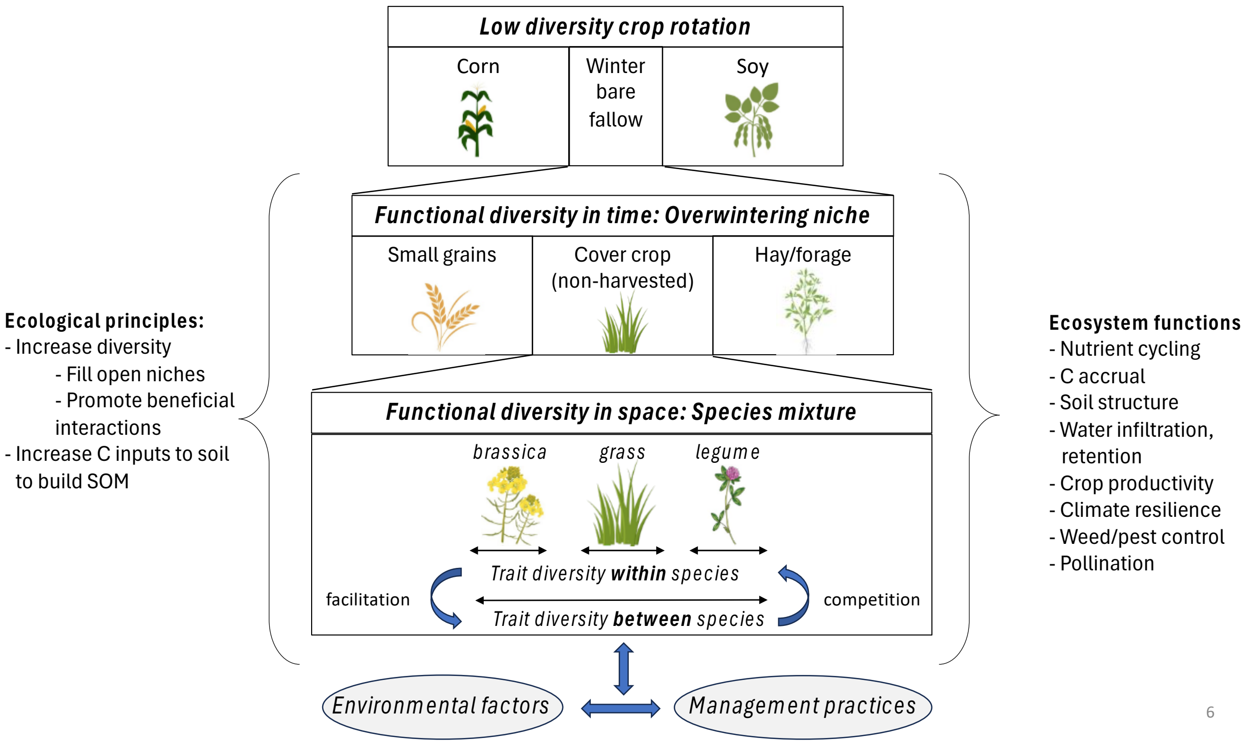

Figure 1-1: Conceptual framework delineating how ecological principles can be applied to agroecosystems in the Great Lakes region to increase ecosystem functions, while also highlighting complex interactions and feedbacks between environmental factors, management practices, and species diversity that influence outcomes on farms.

1.5 Summary of dissertation chapters

Chapter 2: Cover crop functional trait plasticity in response to soil conditions and interspecific interactions. Although overwintering cover crops can support numerous agroecosystem functions, farmers often experience variability in cover crop performance due to a lack of context-specific strategies for optimal cover crop management (Baraibar et al., 2020; Lawson et al., 2015; Murrell et al., 2017; Reiss & Drinkwater, 2020). Further, farmers often select cover crop species based on functional trait contrasts between species, but mounting evidence suggests that functional trait variation within species in response to environmental and management conditions may also be substantial, yet remains understudied (Herrick & Blesh, 2021; Martin et al., 2018; Reiss & Drinkwater, 2018; Siefert et al., 2015). To improve mechanistic and predictive understanding of cover crop trait variation within and across species, I measured nine plant functional traits for cereal rye, crimson clover, and dwarf essex rapeseed across eight farms in a two-year, on-farm experiment. The farms had different management histories that contributed to a gradient of soil health, which I characterized using a suite of biological, chemical, and physical indicators. Because farmers are increasingly combining cover crop species with contrasting and complementary traits in mixtures (CTIC-SARE-ASTA, 2023), I also tested whether trait expression was altered when the cover crops were grown together in mixture relative to monocrop due to interspecific interactions.

Chapter 2 Research Questions:

1) What is the magnitude and relative importance of intraspecific versus interspecific trait variation?

2) Which soil health indicators best explain trait variation?

3) How do interspecific interactions in mixture influence trait variation?

Chapter 2 Hypotheses:

All three cover crop species will show large trait variation across farms, but the importance of intraspecific trait variation relative to interspecific will differ by species and trait. Because cover crops receive little to no inputs during their growing season, soil health indicators of nutrient cycling and availability will explain the greatest trait variation. Trait expression will be significantly modified in mixture due to competitive and facilitative interactions.

Chapter 3: Citizen science reveals opportunities for improving sustainability outcomes of cover crops. Overwintering cover crops are gaining traction as a diversification practice in the Great Lakes region because they can be a feasible and highly effective tool for enhancing agroecosystem function across a variety of farming systems. However, further research is needed to better understand if and how farmers are successfully managing cover crops on their fields given the complex suite of factors that influence cover crop establishment and growth on working farms. Given that many of the benefits from cover crops scale directly with biomass (Blesh, 2018; Finney et al., 2016; MacLaren et al., 2019; McClelland et al., 2021), I developed a field assessment that farmers can perform to estimate cover crop biomass in their fields. When paired with an online management survey completed by partnering farmers, this observational, citizen science approach allows for identifying the extent and drivers of cover crop performance across the Great Lakes region. I specifically focus on cereal rye, which is the most popular cover crop in the region, and multi-species mixtures, which have potential to enhance cover crop productivity, multifunctionality, and resilience (Blesh, 2018; Bybee-Finley et al., 2016; Finney & Kaye, 2017; Wendling et al., 2019).

Chapter 3 Research Questions:

1) What is the extent of variation in cover crop biomass across farm fields?
2) Which environmental and management factors best explain this variation?
3) Do these trends in variation differ between cereal rye and mixtures?

Chapter 3 Hypotheses:

Cereal rye and mixture fields will produce similar levels of biomass, on average, but mixture biomass will be more variable due to greater management complexity despite potential for enhanced performance with higher species diversity. The main factors explaining variation in cover crop performance will differ between the two cover crop types due to differences in plant species and community responses to growing conditions, in part because they may be grown in distinct niches. For instance, mixtures are commonly planted following small grain harvest in late summer, whereas cereal rye is often used following corn or soybean harvest in late fall.

Chapter 4: Diversifying crop rotations with cover crops increases climate resilience on working farms. Increasingly variable and extreme precipitation patterns due to global climate change, including greater frequency of floods and droughts, pose major challenges for agricultural production in the Great Lakes region (Wilson et al. 2023; Trenberth, 2011). Recent analyses of field experiments suggest that increasing crop rotation diversity builds resilience to climate change (Bowles et al., 2020; Degani et al., 2019; Gaudin et al., 2015; Lotter et al., 2003; Marini et al., 2020; Renwick et al., 2021), especially when adding functionally diverse crops with different traits and roles in the ecosystem (Costa et al., 2024; Smith et al., 2023). However, evidence from working farms is lacking. Using a field-scale remote sensing dataset, I tested relationships between crop diversification and agroecosystem climate resilience on working farms in Michigan from 2008 to 2019. I used panel fixed effects regressions and linear regressions to evaluate yield and temporal yield stability (measured as the coefficient of variation), respectively, for corn and soybean in response to 1) an index of crop rotation complexity, and 2) overwintering cover crops. I also used panel fixed effects regressions to test how overwintering cover crops influence corn and soybean planting dates as an indicator of resilience to heavy spring rainfall.

Chapter 4 Research Questions:

1) How do corn and soybean yield and yield stability respond to crop rotation complexity, and more specifically to winter cover crop use?
2) How does winter cover crop use influence corn and soybean planting dates under heavy spring rainfall?
3) How do the effects of past cover crop use (i.e., legacy effects) versus current cover crop status (i.e., immediate effects) on agroecosystem climate resilience differ?

Chapter 4 Hypotheses:

Corn and soybean yield and yield stability will increase with crop rotation complexity, but winter cover crops will have divergent immediate and legacy effects. Specifically, having an overwintering cover crop growing in the spring immediately prior to cash crop planting (i.e., current cover crop status) will negatively impact yield, but cover crop legacy effects will be associated with increased yields and yield stability, particularly after at least three years of cover crop use due to soil quality improvements. Under heavy spring rainfall, immediate and legacy effects will both be positive, such that planting delays will be reduced as years of prior cover crop use increases, and having cover crops growing in the spring immediately prior to cash crop planting will strengthen this effect.

Chapter 5: Conclusions and future directions. In this chapter, I integrate across the three dissertation studies to highlight key takeaways from this research, and note potential limitations. I discuss policy implications, such as the need for monitoring tools to track success of diversification practices, and for greater technical and financial support during early years of transitions to more diverse systems. Finally, I propose ideas for future research that build on the action-oriented and participatory approaches used here to continue improving the science and practice of agroecology for a more sustainable and resilient food system.

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Chapter 2 – Cover Crop Functional Trait Plasticity in Response to Soil Conditions and Interspecific Interactions[1]

Abstract

Cover crops (i.e., non-harvested crops) support ecosystem services in agroecosystems, but their performance can be highly variable. Functional trait ecology provides a useful framework for understanding variation in cover crop performance across different growing conditions. However, most cover crop functional trait research to date has focused on differences between species, leaving trait variation within species poorly understood, despite its potential for significant impacts on agroecosystem functions. In a two-year experiment, we measured nine functional traits for three cover crop species across 13 fields on working farms. Each field contained three cover crop treatments: a functionally diverse mixture of cereal rye (*Secale cereale*), crimson clover (*Trifolium incarnatum*), and dwarf-essex rapeseed (*Brassica napus*), and monocrops of rye and clover. The fields had different management histories and soil properties, creating a gradient of soil health, which integrates physical, chemical, and biological indicators of overall soil function. We evaluated i) the magnitude and relative importance of intraspecific and interspecific trait variation; ii) which soil health indicators best explained trait variation; and iii) whether interspecific interactions in mixture induced trait plasticity. Although there were strong functional trait contrasts between the cover crop species, intraspecific trait variation comprised 50% of total trait variation, on average. Leaf %P and root:shoot ratio

[1] Chapter 2 is prepared for submission to the journal Ecological Applications with co-author Jennifer Blesh.

expressed the largest proportion of intraspecific variation relative to interspecific, and specific leaf area the least. Whole-plant traits, including maximum plant height and root:shoot, showed the greatest magnitude of intraspecific variation. Clover trait variation was best explained by particulate organic matter nitrogen (POM N), soil phosphorus, pH, and permanganate oxidizable carbon; rye trait variation by POM N and soil phosphorus; and dwarf essex trait variation by POM N. Both rye and clover also showed significant trait plasticity in mixture relative to monocrop treatments, likely due to facilitative interactions for rye and competitive interactions for clover. Our study reveals that intraspecific and interspecific trait variation are equally important, and demonstrates that examining trait variation within species can improve understanding of what drives cover crop outcomes across different conditions. This information can then help farmers tailor cover crop management based on context to better meet sustainability goals.

2.1 Introduction

In agroecosystems, cover crops (i.e., non-harvested crops) support numerous ecosystem services critical to sustainable production, such as building soil organic matter (SOM), reducing nutrient losses, and suppressing weeds and pests (Snapp et al. 2005; Schipanski et al. 2014). Functional trait diversity can be a key predictor of ecosystem services from cover crops (Finney and Kaye 2017; Blesh 2018; Storkey et al. 2015). Farmers often select cover crops based on functional contrasts between species, or interspecific diversity, for instance selecting grass species with dense roots for nutrient scavenging, legumes for nitrogen supply via biological nitrogen (N) fixation (BNF), or brassicas with large tap roots to reduce soil compaction. Increasingly, farmers are combining species from these functional groups into multi-species mixtures that can provide multiple services at once (CTIC-SARE-ASTA 2023). At the same time, mounting evidence suggests that, in addition to variation between species, variation within species (i.e., intraspecific trait variation) can also be substantial, not only in natural plant communities (Siefert et al. 2015), but also for managed crops (Martin et al. 2018; Reiss and Drinkwater 2018). This intraspecific variation can then impact agroecosystem function (Gagliardi et al. 2015; Blesh 2018; Hayes et al. 2019). Although appreciation for intraspecific trait variation is growing, including for cover crops (Herrick and Blesh 2021; Reiss and Drinkwater 2022), we lack a thorough understanding of its relative importance compared to interspecific variation, and to which environmental and management factors it is most responsive.

Intraspecific trait variation can reflect plant responses to different abiotic and biotic conditions (Garnier and Navas 2012), including soil health. Soil health can be defined as the capacity of a soil to sustain plants, animals, and humans (NRCS, 2012) and is a comprehensive approach to soil assessment that integrates biological, physical, and chemical indicators of soil function (Doran and Zeiss 2000). Although cover crops can improve soil health (Sharma et al. 2018; Wood and Bowman 2021), their performance may also vary with soil health across farms (Blesh 2018; Bukovsky-Reyes, Isaac, and Blesh 2019). Recent research has identified potential soil health indicators that can predict primary crop performance (e.g., Liptzin et al. 2022; Bagnall et al. 2023), but this approach has not been extended to cover crops. Carbon-based indicators corresponding to soil biological activity, such as mineralizable carbon and permanganate oxidizable carbon, have gained attention given their responsiveness to management, scalability, and relationships with key traits, like yield and drought resilience (Hurisso et al. 2016; O'Neill, Sprunger, and Robertson 2021; Liptzin et al. 2022; Bagnall et al. 2023). Yet compared to harvested crops, cover crops receive few, if any, external inputs, such as fertilizers and irrigation.

For cover crops, then, soil health indicators that reflect soil nutrient cycling and availability may be strong drivers of trait variation and plant performance.

Previous research suggests that soil particulate organic matter (POM) fractions are useful indicators of the quantity and quality of organic matter available for supporting plant growth through nutrient mineralization from microbial decomposition (Cambardella and Elliott 1992; Drinkwater and Snapp 2022). Moreover, because the most popular cover crop functional types – legumes, grasses, and brassicas - have different growth and resource acquisition strategies (Wagg et al. 2021), they may show distinct patterns of trait variation in response to soil health indicators, such as POM. For example, in a previous on-farm cover crop experiment, legume biomass decreased, while non-legume biomass increased, with POM N (Blesh 2018).

Contrasting and complementary characteristics between cover crop species may also influence trait expression when combined in mixture. Legumes can facilitate the growth of non-legumes through the transfer of fixed N (Blesh, VanDusen, and Brainard 2019). Although legumes are often phosphorus (P)-limited in low fertility soils (Isaac et al. 2011; Vitousek et al. 2013; Bargaz et al. 2017), they are also able to support processes that increase soil P availability (Hinsinger et al. 2011; Gallaher and Snapp 2015). This can benefit other species in mixture, but legume performance may still be constrained if those species are superior competitors for soil P despite increased availability overall. Competition for other resources, like water and light can also occur. Quantifying the degree and direction of trait plasticity in response to interspecific interactions can then inform mixture design for multiple functions.

To address gaps in the literature related to patterns of trait variation within and across cover crop species, we established an on-farm experiment to quantify trait variation at the species-level for a functionally diverse mixture of cereal rye (*Secale cereal),* crimson clover

(*Trifolium incarnatum)*, and dwarf-essex rapeseed (*Brassica napus*), and sole-planted rye and clover. These treatments were established on 13 farm fields in Michigan, and selected in partnership with participating farmers to represent desirable cover crop options for the region. The farms had diverse management histories and soil properties that contributed to a gradient of soil health, which we assessed at the beginning of the cover crop growing season using a suite of biological, chemical, and physical indicators. Across this gradient, we address: 1) What is the magnitude and relative importance of intraspecific versus interspecific trait variation? 2) Which soil health indicators best explain trait variation? 3) For rye and clover, how do interspecific interactions in mixture influence trait variation? We hypothesize that: 1) all three cover crop species will show large trait variation across farms, and that the importance of intraspecific trait variation will vary by species and trait; 2) because cover crops receive little to no inputs during their growing season, indicators of soil nutrient cycling and availability, such as POM N and soil P, will explain the greatest trait variation; and 3) trait expression for rye and clover will be significantly modified in mixture due to interspecific interactions like competition and facilitation.

2.2 Methods

2.2.1 Experimental design

We tested our hypotheses in a two-year on-farm experiment in Michigan from 2020-2022. Field sites included seven grain farms in Tuscola County, MI, and the Kellogg Biological Station (KBS) in Hickory Corners, MI. Each farm selected one field to include in the study per year (i.e., a different field in each year); however, due to early termination, two fields were dropped during the first year, and one field was dropped during the second year, resulting in 13 total fields across the two study years. The farms ranged from several decades of organic management to those recently beginning the transition to organic management. We selected the Tuscola County (Thumb region) and KBS field sites for this study because they were similar farm types (i.e., diversified grain farms), and had distinct management histories that contributed to a gradient of soil health.

In August 2020 and August 2021, following harvest of a small grain crop, three cover crop treatments were planted with a grain drill in a randomized complete block design with four replicates in each farm field, except for one farm field in year two, which only contained three blocks due to space constraints. Treatments included a cereal rye (*Secale cereal)*, crimson clover (*Trifolium incarnatum)*, dwarf-essex rapeseed (*Brassica napus*), and oat (*Avena sativa*) mixture, and rye and crimson clover monocultures. A dwarf-essex monoculture was not included because sole-planted brassica cover crops are not common in this region, and farmers expressed greater interest in using the experiment to generate data on practical cover crop treatments. Additionally, because the oats winter-killed, and our trait sampling occurred in the spring, oats are not included in this analysis. Rye and clover were seeded at rates of 101 kg ha^{-1} and 16.8 kg ha^{-1} in monocrop treatments, and 22.4 kg ha^{-1} and 9.0 kg ha^{-1} in the mixture, respectively. Dwarf essex in mixture was planted at 2.2 kg ha^{-1}, and oats at 28.0 kg ha^{-1}. Plot dimensions were 36.5 x 5.5 m. We established plots in relatively flat areas of each field to minimize the effects of topography on soil resource availability and plant growth (Kravchenko et al. 2005). All cover crop plots were rainfed and received no additional fertility amendments throughout their growing season.

2.2.2 Soil health gradient

In September 2020 and 2021, three weeks after cover crop planting, we collected plot-level soil samples for in-depth analysis of soil health indicators. In each plot, we composited 6 soil cores each taken to 20 cm depth using a 2 inch Dutch auger. Following 2-5 days of storage at 4°C, soil samples were processed for soil moisture and extractable inorganic N (NO_3^- and NH_4^+). Triplicate soil subsamples were sieved to 2 mm for inorganic N determination and for a 7-day anaerobic N mineralization incubation (potentially mineralizable N (PMN)) (Drinkwater et al. 1997), followed by extraction with 2 M KCl. The amount of inorganic N in each sample was analyzed colorimetrically on a continuous flow analyzer (AQ2; Seal Analytical, Mequon, WI). Remaining soil was air-dried before further analysis. We measured total soil C and N by dry combustion on a Leco TruMac CN Analyzer (Leco Corporation, St. Joseph, MI), as well as short-term C-mineralization (potentially mineralizable carbon; PMC) and permanganate oxidizable carbon (POXC), which are indicators of more active soil C pools than total soil C (Culman et al. 2012; Franzluebbers et al. 2000). We determined light fraction (i.e., "free") particulate organic matter (fPOM) and occluded POM (i.e., physically protected inside soil aggregates; oPOM) using both size and density fractionation techniques for triplicate 40 g subsamples, as described in Blesh (2019). The C and N content of fPOM and oPOM fractions were measured on a Costech ECS 4010 CHNS Analyzer (Costech Analytical, Valencia, CA). Soil subsamples were also analyzed at A&L Great Lakes Laboratories, Inc. (Fort Wayne, IN) for a standard soil test including macro- and micro-nutrients, texture, and pH. Bulk density was calculated from the fresh weight of three, 5 cm diameter cores per block and adjusted for soil moisture.

2.2.3 Functional trait field sampling

In May 2021, each species in each treatment was sampled for multiple functional traits related to how plants acquire, conserve, and influence the availability of resources in their environment, including maximum plant heights (cm), specific leaf area (SLA) (cm^2 g^{-1}), leaf %N and %P, shoot and root C:N, root:shoot ratio (R:S), and root %N and %P (Garnier and Navas 2012; Wilke and Snapp 2008; Wright et al. 2004). In each plot, we collected aboveground biomass from two 0.25 m^2 quadrats by clipping all plant material at the ground surface and separating by species, except for weeds which were grouped into one category. For SLA, we collected leaves from nine individuals per species per plot. To estimate root biomass and quantify root:shoot ratios, in each plot we collected six 7 cm diameter cores to 20 cm depth, which we believe captured the majority of belowground biomass for these annual cover crop species (Robertson 1999; Amsili and Kaye 2021). Three cores were taken in-row directly over cover crop plants (one per species in mixture), and the remaining three were taken in between cover crop rows to capture lateral roots. Roots were then gently washed using a sieving method, capturing all roots >1 mm. For mixtures, we isolated the dwarf essex taproots but were unable to separate the rye and clover roots. We therefore measured root traits at the species-level for sole-planted rye and clover and for dwarf essex in mixture. The procedures described above were repeated in the second year of the experiment in May 2022.

2.2.4 Functional trait analysis

Root, shoot, and leaf samples were dried at 60°C for 48 hours, ground to <2 mm, and analyzed for %C and N on a Leco TruMac autoanalyzer (Leco Corporation, St. Joseph, MI). Prior to drying and weighing, leaves were photographed and processed using ImageJ software to calculate fresh leaf surface area. We ashed all dried root samples to correct biomass weights for any mineral soil that had not been removed during washing. To determine leaf and root tissue %P, we ashed and then digested samples with nitric acid, followed by analysis using inductively coupled plasma spectroscopy (ICP-OES; Perkin Elmer, Inc., Waltham, MA). We estimated R:S for each species by scaling root biomass to units of kg ha^{-1} based on the surface area of the root cores, and then dividing by aboveground cover crop biomass (kg ha^{-1}) (Amsili and Kaye 2021).

2.2.5 Statistical analysis

All statistical analyses were performed in R v. 4.2.1 (R Foundation for Statistical Computing, Vienna, Austria). To initially evaluate patterns of trait variation within and across species in multivariate space, we performed a principal component analysis (PCA). We then assessed the magnitude of inter- and intraspecific trait variation for each trait by calculating coefficients of variation (CV) within and across species, along with means and ranges. Following Leps et al. (2006), we used variance partitioning to quantify the extent of intraspecific trait variation relative to interspecific trait variation. This was calculated individually for each trait, where intraspecific variance is the average of within-species variances, interspecific variance is the variance of species-level mean trait values, and total variance is the sum of the two.

Using the '*lme4*' package, we identified key drivers of trait variation with mixed effects models. Specifically, we tested the relative importance of six soil health indicators selected based on hypotheses, previous research, and PCA loadings: PMC, POXC, oPOM N, pH, Bray-1 P, and % clay. Correlation matrices and PCA confirmed that they represent unique components of soil health (Figure S2-6; Table S2-6). PMC and POXC are both indicators of active soil C fractions, but PMC may be more reflective of short-term organic matter mineralization, while POXC reflects longer-term C stabilization (Hurisso et al. 2016). Although oPOM N is similar to PMC and POXC in that it is also an indicator of labile organic matter pools, oPOM N more closely reflects soil organic matter quality and N cycling capacity (Cambardella and Elliott 1992; Wander 2004; Blesh 2019), and supports other soil functions, like soil aggregate stability (Drinkwater and Snapp 2022). Soil pH and Bray-1 P are chemical indicators of soil health, and clay is included as a soil physical property, but can also influence nutrient availability through effects on cation exchange capacity.

All trait models included year as a fixed effect, and block nested in farm as random effects. We added planting treatment as a fixed effect in models of rye and clover aboveground traits, which were measured in both mixture and monocrop. We also performed separate regressions for rye and clover aboveground traits in mixture versus monocrop to determine if trait responses to soil conditions differed between planting treatments. One field was excluded from the regression analyses because it was a Histosol (i.e., "muck" soil mainly comprised of organic materials), with soil properties related to organic matter being strong outliers. We also excluded one R:S outlier each for rye and clover and three for dwarf essex, and one rye height outlier. Additionally, several dwarf essex root and shoot samples were too small for some of the chemical analyses, resulting in slightly smaller sample sizes for those traits. Explanatory variables were centered to a mean of 0, and response variables were log transformed to meet assumptions of normality and homoskedasticity and to enable calculating the expected percentage change for each trait in response to significant model terms. For significant soil properties, the percentage change is the predicted effect on a trait when moving from the minimum to maximum value for a given soil property across the gradient, while holding all other variables constant. For planting treatment, the percentage change is the expected change in mixture compared to monocrop, while holding all other variables constant.

2.3 Results

2.3.1 Interspecific trait variation

As expected, the three cover crop species showed strong functional trait contrasts (Table 2-1). Dwarf essex was, on average, 3- and 1.5-times taller than clover and rye, respectively.

Clover had the lowest mean shoot and root C:N, and highest mean leaf and root N, while dwarf essex had the highest mean leaf and root P. Both rye and dwarf essex had a mean R:S greater than one, indicating there was more biomass belowground than aboveground for those species. When evaluating patterns of variation for all nine traits using PCA, the three cover crop species clearly occupied distinct areas of multivariate trait space (Figure 2-1). High leaf and root N for clover on one end of PC 1, which explained 47.6% of variation, opposed tall height and high shoot and root C:N for dwarf essex on the other, with rye situated in between (Table S2-7). PC 2, which explained an additional 21.4% of variation, had the highest loadings for leaf and root P for dwarf essex, and to a lesser extent rye and dwarf essex R:S, in opposition to high SLA for clover. However, each species also showed substantial spread across multivariate trait space, indicating plasticity in functional trait strategies due to intraspecific variation.

Table 2-1: Descriptive statistics for cover crop functional traits within and across species.

	Rye				*Clover*				*Dwarf essex*			
Trait	Mean	Range	CV (%)	N	Mean	Range	CV (%)	N	Mean	Range	CV (%)	N
Height (cm)	37.3	8.44-72.1	32.8	102	16.2	3.80-44.2	68.6	102	51.2	12.6-98.2	56.3	51
Shoot C:N	22.9	9.67-39.6	28.5	102	14.5	10.3-21.7	15.4	102	18.6	11.9-26.1	22.6	48
Root C:N	29.3	21.8-41.0	15.7	51	19.5	15.8-25.4	12.0	51	38.9	13.5-70.1	37.3	48
R:S	2.71	0.37-8.86	67.5	50	0.99	0.31-3.67	72.4	50	1.65	0.34-4.61	69.7	46
SLA (cm^2/g)	225	185-284	10.1	102	298	205-384	14.0	102	144	76.3-208	20.2	51
Leaf %N	3.01	2.14-4.96	20.9	102	4.28	2.90-5.30	12.1	102	3.21	2.30-5.1	22.1	51
Root %N	1.20	0.88-1.60	15.5	51	2.10	1.45-2.55	12.2	51	1.24	0.60-2.90	44.9	48
Leaf %P	0.49	0.25-0.76	24.2	102	0.38	0.21-0.55	20.7	102	0.50	0.32-0.78	27.9	51
Root %P	0.25	0.16-0.33	17.6	51	0.36	0.16-0.77	32.8	51	0.46	0.25-0.86	26.2	49

CV = coefficient of variation; Shoot C:N = shoot carbon:nitrogen; root C:N = root carbon:nitrogen; R:S = root:shoot ratio; SLA = specific leaf area.

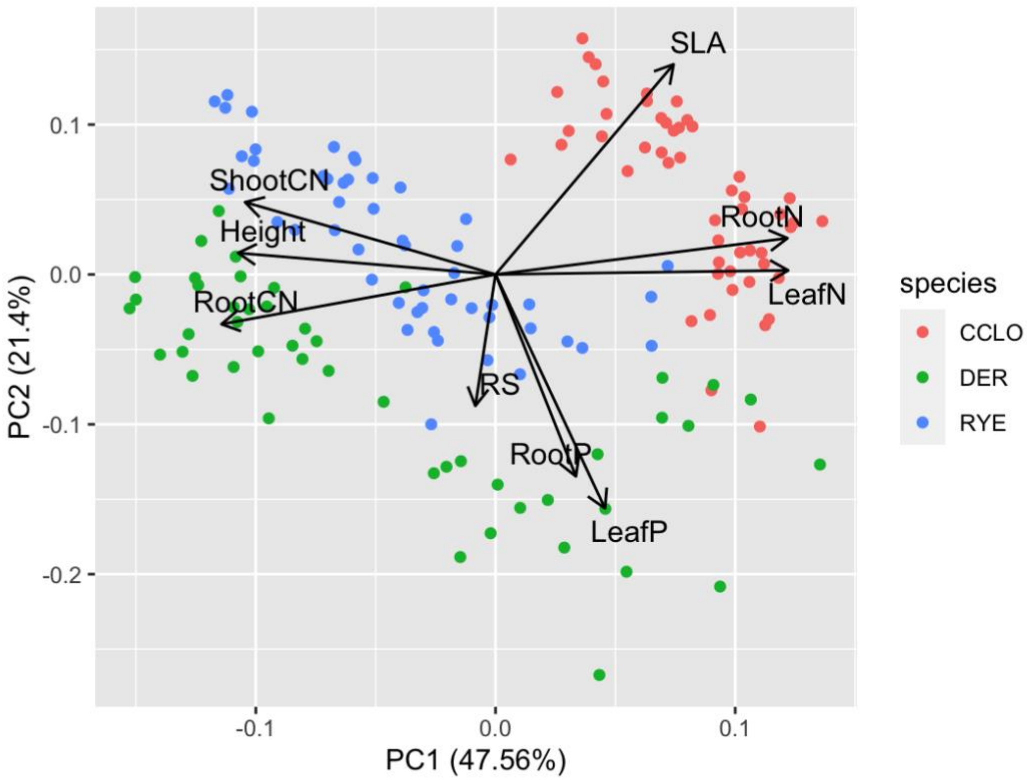

Figure 2-1: Principal component analysis of nine functional traits across three cover crop species. CCLO = crimson clover; DER = dwarf essex rapeseed; RYE = cereal rye; SLA = specific leaf area; shoot C:N = shoot carbon:nitrogen; root C:N = root carbon:nitrogen; RS = root:shoot ratio; root P = root phosphorus; leaf P = leaf phosphorus; leaf N = leaf nitrogen; root N = root nitrogen.

2.3.2 Intraspecific trait variation

Variance partitioning revealed that, on average, intraspecific trait variation comprised 49.9% of total trait variation, though its importance differed by trait (Figure 2-2). Relative to interspecific variation, intraspecific variation was most important for leaf P and R:S, and least important for SLA (Figure 2-2). Although a high proportion of total variance in leaf P was explained by intraspecific variation (77.4%), the magnitude of intraspecific variation was relatively small compared to R:S, with the intraspecific CV for leaf P being roughly one-third of that for R:S on average across species (Figure 2-3). Intraspecific CV was greatest for the two whole-plant traits – R:S and height. For some traits, the degree of intraspecific variation differed between species (Figure 2-3; Table 2-1). Clover had a consistently lower CV than rye and dwarf essex for chemical traits related to N, and for leaf P, but not root P, for which clover was most variable. Dwarf essex showed twice as much variation in root C:N as rye and clover, and variation in height for rye was roughly half that for clover and dwarf essex. Notably, the magnitude of intraspecific trait variation for rye and clover was similar when mixture and monocrop planting treatments were combined compared to when these treatments were evaluated separately (Figure S2-7).

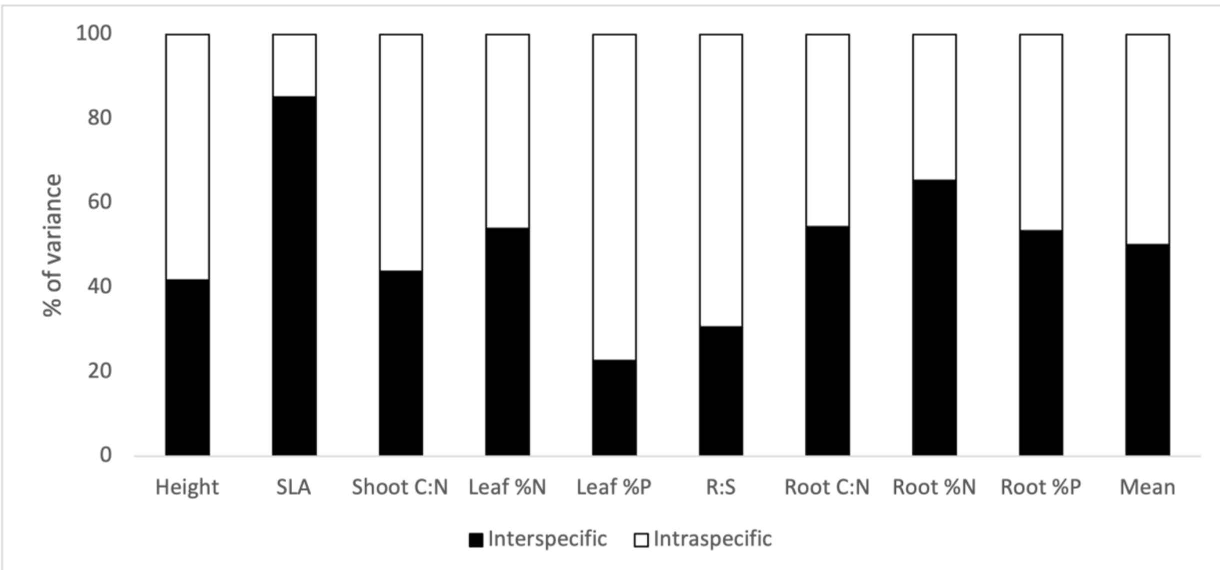

Figure 2-2: Contributions of interspecific and intraspecific trait variation to total trait variation (%) for nine cover crop functional traits, plus the mean across all nine traits. SLA = specific leaf area; shoot C:N = shoot carbon:nitrogen; R:S = root:shoot ratio; root C:N = root carbon:nitrogen.

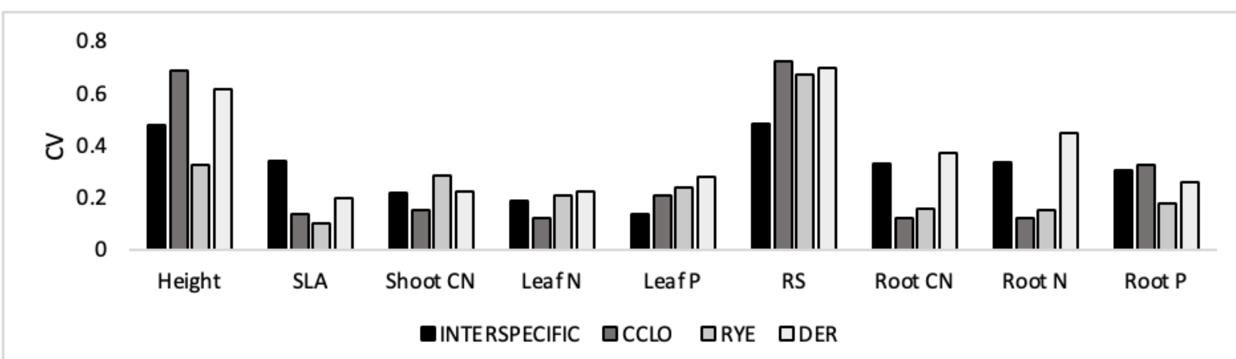

Figure 2-3: Magnitude of variation, shown here as the coefficient of variation (CV), for all above- and belowground functional traits within (intraspecific) and across (interspecific) species. CCLO = crimson clover; DER = dwarf essex rapeseed; SLA = specific leaf area; shoot CN = shoot carbon:nitrogen; RS = root:shoot ratio.

2.3.3 Trait variation in response to soil properties

Soil properties varied widely across fields, reflecting a gradient of soil health (Table 2-2). Biological indicators of soil N cycling were particularly variable, with oPOM N, PMN, and fPOM N varying 5-, 6- and 8-fold across fields, though PMC and POXC also varied 3- and 2.5-fold, respectively. Soil inorganic N (NH_4^+ + NO_3^-) concentrations were low overall (5.5 mg kg^{-1}, on average). Plant-available P ranged from 24-211 mg kg^{-1} across fields. Despite being located in the same county, the field sites also had considerable variation in soil texture, with clay ranging from 2.2-36.6% and sand from 35.4-84.8%. Soils were neutral to alkaline, with a mean pH of 7.4 and range of 5.9-8.0.

We found trait- and species-specific responses to soil health indicators (Table 2-3, Table 2-4). Clover trait variation was best explained by particulate organic matter nitrogen (POM N), soil phosphorus, pH, and permanganate oxidizable carbon; rye trait variation by POM N and soil phosphorus; and dwarf essex trait variation by POM N (Figure 2-4). Soil texture was also a significant predictor in some cases, particularly for the two whole plant traits, R:S and height.

For clover, an increase in POXC from 314 to 784 mg kg^{-1} across fields was associated with 28% lower height ($p=0.04$), 19% lower shoot C:N ($p=0.006$), and 9% lower root P ($p=0.002$), and increases in leaf N and R:S of 14% ($p<0.001$) and 47% ($p=0.002$), respectively. Across the gradient, increasing oPOM N corresponded with higher SLA (28%; $p<0.001$), leaf N (21%; $p<0.001$), and leaf P (7%; $p=0.002$), and lower shoot C:N (-35%; $p<0.001$) for clover. Clover root N, leaf P, and root P increased by 19% ($p=0.002$), 11% ($p<0.001$), and 37% ($p<0.001$) in response to soil P, respectively, while root C:N decreased by 37% ($p<0.001$). As pH changed from 5.9 to 8.0, clover leaf N was reduced by 24% ($p=0.002$) and R:S by 47% ($p=0.02$), while shoot C:N increased by 24% (p=0.04). Clover R:S responded negatively to %clay (-34%; p=0.005), but leaf P showed a small, positive response (7%; p=0.01).

Table 2-2: Descriptive statistics for soil health properties across field sites. N = 141 for all soil properties except bulk density and POXC, where N = 47 because those properties were measured at the block, rather than plot scale.

Soil Properties		**Unit**	**Mean**	**Range**
Biological	PMN	mg kg^{-1} wk^{-1}	5.8	2.0 - 12.7
	PMC	µg CO_2-C g^{-1} day^{-1}	29.3	17.8 - 54.4
	POXC	mg kg^{-1}	549	314-784
	fPOM N	mg kg^{-1}	35.9	10.9 - 92.1
	oPOM N	mg kg^{-1}	42.5	17.8 - 87.7
Chemical	inorganic N	mg kg^{-1}	5.5	1.1 - 17.0
	pH		7.4	5.9 - 8.0
	Bray-1 P	mg kg^{-1}	81.8	24 - 211
	K	mg kg^{-1}	146.5	46 - 234
	Mg	mg kg^{-1}	244.2	55 - 450
	Ca	mg kg^{-1}	1855.1	550 - 2900
	CEC		11.8	4.5 - 18.2
	total C	g kg^{-1}	13.4	8.1 - 20.7
	total N	g kg^{-1}	1.3	0.7 - 1.9
Physical	bulk density	g cm^3	1.5	1.0 - 1.8
	sand	%	53.2	35.4 - 84.8
	silt	%	31.0	11.4 - 52.6
	clay	%	15.7	2.2 - 36.6

PMN = potentially mineralizable nitrogen; PMC = potentially mineralizable carbon; fPOM = free particulate organic matter; oPOM = occluded particulate organic matter; CEC = cation exchange capacity.

In response to oPOM N, there were decreases in rye height (-49%; p<0.001), shoot C:N (-63%; p<0.001), and root C:N (-28%; p=0.04), and increases in SLA (35%; p<0.001), leaf N (49%; p<0.001), leaf P (21%; p<0.001), root P (7%; p=0.007), and R:S (71%; p=0.02). Interestingly, the only rye trait that was not significantly related to oPOM N was root N, which instead responded negatively to pH (-16%; p=0.02). The soil P gradient was associated with increases in rye R:S (113%; p=0.002), leaf N (19%; p<0.001), leaf P (11%; p=0.002), and root P (9%; p<0.001), and a decrease in rye shoot C:N (-56.1%; p<0.001). There was a 102% reduction in rye R:S as clay increased from 2-37% across fields (p=0.01). Conversely, rye height increased by 35% with clay (p=0.02).

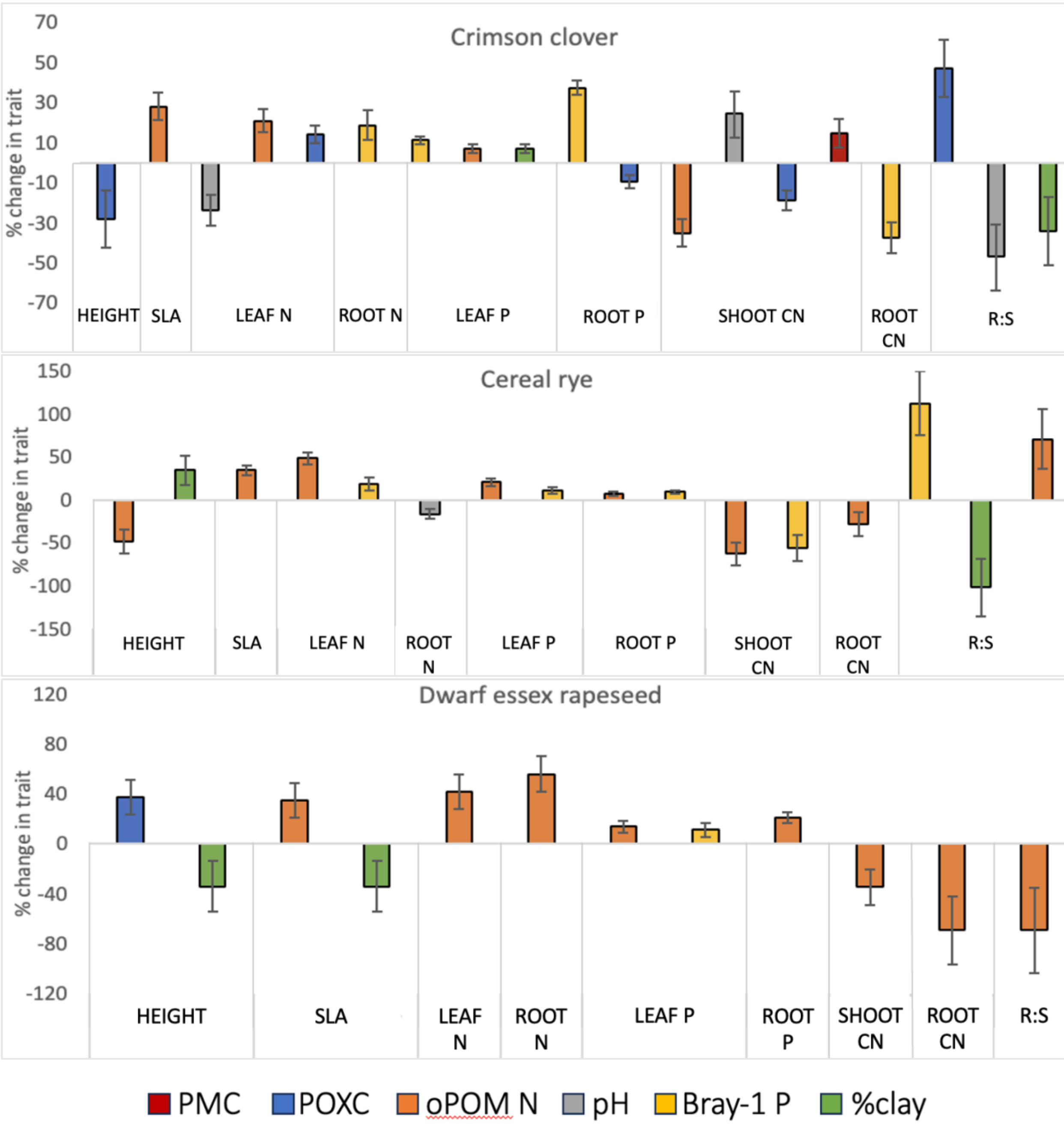

Figure 2-4: Expected percentage change in cover crop functional traits in response to significant soil health parameters at α < 0.05 based on regression models (Tables 2-3 and 2-4). The "% change in trait" represents the expected change from the minimum to maximum value for each soil property across the 12 field sites. SLA = specific leaf area; CN = carbon:nitrogen; RS = root:shoot ratio.

Table 2-3: Regression coefficients (± standard error) for mixed models of aboveground traits. Coefficients in bold are significant at $\alpha<0.05$.

CLOVER	**log(Height)**		**log(SLA)**		**log(Leaf %N)**		**log(Leaf %P+1)**		**log(Shoot C:N)**	
Intercept	**3.06**	(0.14)	**5.88**	(0.03)	**1.49**	(0.04)	**0.31**	(0.01)	**2.59**	(0.06)
PMC	0.004	(0.003)	0.001	(0.002)	-0.001	(0.001)	0.0004	(0.0004)	**0.004**	(0.002)
POXC	**-0.0006**	(0.0003)	0.0002	(0.0001)	**0.0003**	(0.00009)	-0.00001	(0.00003)	**-0.0004**	(0.0001)
oPOMN	-0.003	(0.002)	**0.004**	(0.001)	**0.003**	(0.0008)	**0.001**	(0.0003)	**-0.005**	(0.001)
pH	-0.15	(0.11)	-0.02	(0.03)	**-0.12**	(0.04)	0.009	(0.01)	**0.11**	(0.05)
P_B1	0.0002	(0.0008)	-0.0006	(0.0003)	-0.0002	(0.0003)	**0.0006**	(0.0001)	-0.0007	(0.0004)
%clay	0.009	(0.005)	-0.001	(0.002)	-0.0005	(0.002)	**0.002**	(0.0006)	0.0001	(0.002)
Trt	**-0.33**	(0.05)	**-0.08**	(0.03)	**-0.04**	(0.02)	**-0.02**	(0.007)	**0.07**	(0.02)
Year	**-1.10**	(0.07)	**-0.24**	(0.03)	**0.07**	(0.02)	**0.08**	(0.009)	-0.06	(0.03)
Trt*Year	0.14	(0.07)	**0.14**	(0.04)	**-0.06**	(0.02)	-0.02	(0.009)	-0.02	(0.03)
Marg. R^2	0.68		0.57		0.36		0.64		0.36	
Cond. R^2	0.94		0.58		0.86		0.85		0.83	
RYE	**log(Height)**		**log(SLA)**		**log(Leaf %N)**		**log(Leaf %P+1)**		**log(Shoot C:N)**	
Intercept	**3.40**	(0.13)	**5.56**	(0.04)	**1.22**	(0.09)	**0.42**	(0.03)	**3.00**	(0.12)
PMC	0.00007	(0.002)	-0.0002	(0.001)	-0.002	(0.002)	-0.001	(0.0009)	0.003	(0.003)
POXC	-0.0003	(0.0002)	-0.0002	(0.0001)	-0.0001	(0.0001)	0.00008	(0.00007)	-0.0001	(0.0003)
oPOMN	**-0.007**	(0.002)	**0.005**	(0.0008)	**0.007**	(0.001)	**0.003**	(0.0006)	**-0.009**	(0.002)
pH	-0.10	(0.08)	0.006	(0.03)	-0.04	(0.06)	0.02	(0.03)	0.002	(0.10)
P_B1	0.0007	(0.0006)	-0.0001	(0.0003)	**0.001**	(0.0004)	**0.0006**	(0.0002)	**-0.003**	(0.0008)
%clay	**0.01**	(0.005)	-0.003	(0.002)	-0.005	(0.003)	-0.0006	(0.002)	0.01	(0.006)
Trt	-0.006	(0.04)	-0.02	(0.03)	**0.05**	(0.03)	**0.06**	(0.01)	**-0.16**	(0.06)
Year	-0.05	(0.06)	**-0.10**	(0.03)	-0.01	(0.04)	0.03	(0.02)	-0.06	(0.08)
Trt*Year	-0.04	(0.05)	-0.005	(0.03)	-0.03	(0.04)	-0.03	(0.02)	-0.01	(0.07)
Marg. R^2	0.13		0.38		0.22		0.31		0.28	
Cond. R^2	0.90		0.72		0.89		0.80		0.76	
DWARF ESSEX	**log(Height)**		**log(SLA)**		**log(Leaf %N)**		**log(Leaf %P+1)**		**log(Shoot C:N)**	
Intercept	**3.99**	(0.20)	**4.15**	(0.08)	**1.17**	(0.07)	**0.39**	(0.03)	**2.90**	(0.09)
PMC	-0.007	(0.003)	0.003	(0.003)	-0.0003	(0.003)	-0.000002	(0.001)	0.0002	(0.003)
POXC	**0.0008**	(0.0003)	-0.0001	(0.0003)	-0.0003	(0.0002)	-0.0001	(0.00008)	-0.00007	(0.0002)
oPOMN	0.0008	(0.003)	**0.005**	(0.002)	**0.006**	(0.002)	**0.002**	(0.0007)	**-0.005**	(0.002)
pH	0.18	(0.14)	0.05	(0.08)	-0.01	(0.07)	0.02	(0.03)	0.03	(0.12)
P_B1	0.002	(0.001)	-0.0008	(0.0009)	0.0009	(0.0008)	**0.0006**	(0.0003)	-0.0007	(0.0008)
%clay	**0.02**	(0.007)	**-0.01**	(0.006)	-0.003	(0.005)	-0.00003	(0.002)	-0.005	(0.006)
Year	**-0.91**	(0.07)	-0.19	(0.07)	**0.17**	(0.06)	**0.10**	(0.02)	**-0.24**	(0.06)
Marg. R^2	0.56		0.34		0.46		0.45		0.32	
Cond. R^2	0.98		0.63		0.73		0.85		0.83	

SLA = specific leaf area; C:N = carbon:nitrogen; Marg = marginal; Cond = conditional. Trt = treatment, where a positive slope means the trait increased in mixture relative to monocrop.

Table 2-4: Regression coefficients (+/- standard error) for mixed models of belowground traits. Coefficients in bold are significant at α<0.05.

CLOVER	**log(Root %N)**		**log(Root %P+1)**		**log(Root C:N)**		**log(RS+1)**	
Intercept	**0.62**	(0.04)	**0.23**	(0.02)	**3.04**	(0.04)	**0.62**	(0.09)
PMC	-0.0004	(0.002)	0.0002	(0.0008)	0.0004	(0.002)	-0.006	(0.004)
POXC	-0.00008	(0.0002)	**-0.0002**	(0.00007)	0.0002	(0.0001)	**0.001**	**(0.0003)**
oPOMN	0.0007	(0.001)	0.0004	(0.0006)	-0.001	(0.001)	0.004	(0.003)
pH	-0.08	(0.05)	0.03	(0.02)	0.05	(0.04)	**-0.25**	(0.10)
P_B1	**0.001**	(0.0004)	**0.002**	(0.0002)	**-0.002**	(0.0004)	-0.0004	(0.001)
%clay	0.0004	(0.002)	0.002	(0.001)	0.0008	(0.002)	**-0.02**	(0.005)
Year	**0.19**	(0.03)	**0.11**	(0.01)	**-0.15**	(0.03)	**0.30**	(0.07)
Marginal R^2	0.49		0.70		0.48		0.58	
Conditional R^2	0.77		0.89		0.72		0.79	
RYE	**log(Root %N+1)**		**log(Root %P+1)**		**log(Root C:N)**		**log(RS+1)**	
Intercept	**0.81**	(0.03)	**0.23**	(0.01)	**3.23**	(0.07)	**1.35**	(0.18)
PMC	0.0007	(0.002)	-0.0006	(0.0007)	0.002	(0.003)	-0.01	(0.008)
POXC	0.0001	(0.0001)	-0.00006	(0.00005)	0.0002	(0.0003)	0.0001	(0.0006)
oPOMN	0.0003	(0.001)	**0.001**	(0.0004)	**-0.004**	(0.002)	**0.01**	(0.005)
pH	**-0.08**	(0.03)	0.02	(0.01)	-0.009	(0.07)	-0.09	(0.17)
P_B1	0.0004	(0.0004)	**0.0005**	(0.0001)	-0.0008	(0.0007)	**0.006**	(0.002)
%clay	-0.004	(0.003)	0.00006	(0.0009)	0.009	(0.005)	**-0.03**	(0.01)
Year	-0.02	(0.03)	0.001	(0.01)	0.09	(0.06)	0.07	(0.14)
Marginal R^2	0.36		0.44		0.15		0.35	
Conditional R^2	0.42		0.55		0.57		0.78	
DWARF ESSEX	**log(Root %N+1)**		**log(Root %P+1)**		**log(Root C:N)**		**log(RS+1)**	
Intercept	**0.83**	(0.07)	**0.45**	(0.04)	**3.57**	(0.13)	**0.39**	(0.12)
PMC	0.002	(0.004)	-0.0006	(0.0008)	0.0002	(0.006)	0.002	(0.009)
POXC	-0.0003	(0.0003)	0.000007	(0.00007)	0.0007	(0.0005)	-0.0004	(0.0006)
oPOMN	**0.008**	(0.002)	**0.003**	(0.0006)	**-0.01**	(0.004)	**-0.01**	(0.005)
pH	-0.04	(0.11)	-0.05	(0.04)	0.16	(0.19)	-0.17	(0.17)
P_B1	0.0002	(0.0009)	0.0004	(0.0002)	-0.002	(0.002)	-0.002	(0.002)
%clay	-0.0009	(0.006)	0.0008	(0.002)	-0.005	(0.01)	0.02	(0.01)
Year	**0.18**	(0.07)	0.03	(0.02)	-0.43	(0.12)	**0.53**	(0.14)
Marginal R^2	0.49		0.26		0.53		0.44	
Conditional R^2	0.69		0.96		0.71		0.44	

Root C:N = root carbon:nitrogen; RS = root:shoot.

All dwarf essex traits except height had significant associations with oPOM N. Specifically, there was an increase of 35% for SLA (p=0.02), 42% for leaf N (p=0.002), 56% for root N (p=0.002), 14% for leaf P (p=0.02), and 21% for root P (p<0.001), while shoot C:N, root C:N, and R:S decreased by 35% (p=0.02), 70% (p=0.003), and 70% (p=0.01), respectively. The only dwarf essex trait that responded significantly to soil P was leaf P, which increased by 11% (p=0.04). With increasing clay, dwarf essex had 70% greater height (p=0.007) and 34% lower

SLA (p=0.02). Finally, there was a positive relationship between POXC and dwarf essex height, corresponding to an increase of 38% across the gradient (p=0.006).

2.3.4 Trait variation in response to planting treatment

All five clover aboveground traits and three rye aboveground traits differed significantly between planting treatments (Figure 2-5). Clover height and SLA decreased by 28% (p<0.001) and 7.7% (p=0.009), respectively, in mixture relative to monocrop, but those traits did not show significant differences for rye (Table 2-3; Figure 2-5). Rye and clover leaf N showed opposite responses to planting treatment, with rye leaf N 5% higher (p=0.05), and clover leaf N 4% lower (p=0.02), in mixture compared to monocrop. Conversely, shoot C:N was 15% lower for rye, and 7% higher for clover, in mixture (p=0.006 and p=0.008, respectively). Clover leaf P was slightly lower in mixture (-2%; p=0.02), while rye leaf P was higher in mixture (6%; p<0.001).

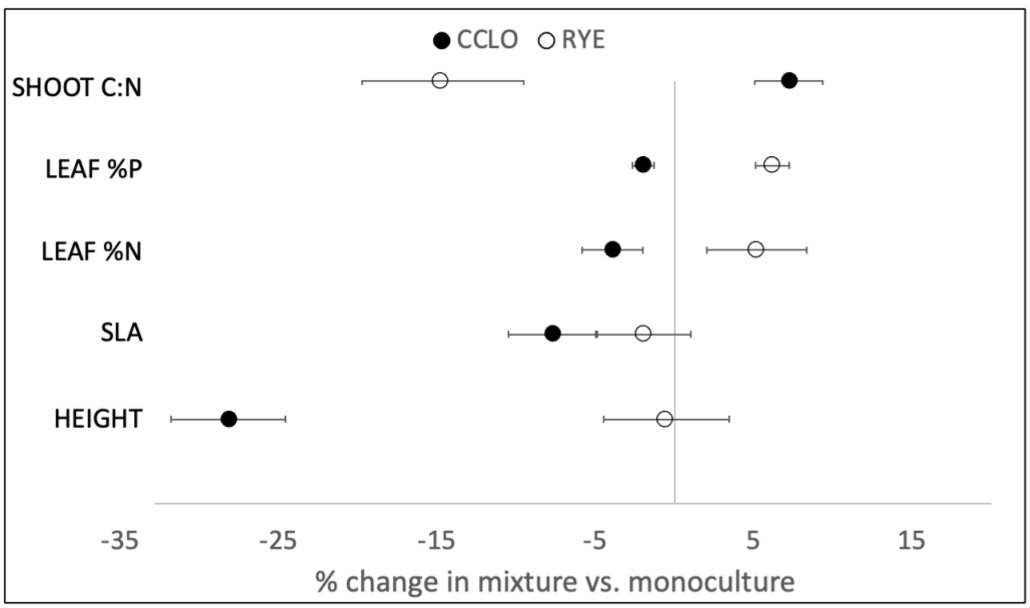

Figure 2-5: Predicted percent change in crimson clover (CCLO) and cereal rye (RYE) aboveground functional traits when grown in mixture relative to monoculture based on regression model results. Shoot C:N = shoot carbon:nitrogen; SLA = specific leaf area.

In some cases, aboveground traits for rye and clover responded differently to soil properties when mixture and monocrop were evaluated separately (Table 2-5). While clover height did not respond significantly to any soil properties in mixture, it decreased with increasing POXC in monocrop (p=0.004) (Table S2-8). Clover SLA showed the opposite pattern - increasing with POXC in mixture (p=0.007), but no relationship in monocrop. Leaf N for clover in mixture decreased with pH (p<0.001) and increased with POXC (p<0.001), but those soil properties did not explain variation in monocrop. There was a positive relationship between %clay and clover leaf P in monocrop (p=0.03), but not mixture. For rye in monocrop, height increased significantly with clay (p=0.02), and SLA decreased with Bray-1 P (p=0.01), but those relationships were not significant in mixture (Table S2-9). While oPOM N was the only significant soil predictor for rye leaf N in mixture (p<0.001), in monocrop rye leaf N increased with both oPOM N and Bray-1 P (p=0.003), and decreased with pH (p=0.04) and % clay (p=0.05). Finally, there was a positive relationship between rye leaf P and Bray-1 P (p=0.004) in monocrop, but not in mixture.

Table 2-5: Comparison of significant predictors of clover and rye aboveground trait variation across regression models. 'Combined' refers to regression models that include both mixture and monocrop trait data, with treatment as a fixed effect along with soil properties, whereas "Mixture" and "Monocrop" are models in which the two treatments were analyzed separately. (+) indicates a positive relationship; (-) indicates a negative relationship. For treatment, the directionality is for traits in mixture relative to monocrop.

	CLOVER			RYE		
	Regression model			*Regression model*		
Trait	Combined	Mixture	Monocrop	Combined	Mixture	Monocrop
Height	Treatment (-) POXC (-)	None	POXC (-)	oPOM N (-) % clay (+)	oPOM N (-)	oPOM N (-) % clay (+)
SLA	Treatment (-) oPOM N (+)	oPOM N (+) POXC (+)	oPOM N (+)	oPOM N (+)	oPOM N (+)	oPOM N (+) Bray-1 P (-)
Leaf N	Treatment (-) oPOM N (+) POXC (+) pH (-)	oPOM N (+) POXC (+) pH (-)	oPOM N (+)	oPOM N (+) Bray-1 P (+)	oPOM N (+)	oPOM N (+) Bray-1 P (+) pH (-) % clay (-)
Leaf P	Treatment (-) Bray-1 P (+) oPOM N (+) % clay (+)	Bray-1 P (+) oPOM N (+)	Bray-1 P (+) oPOM N (+) % clay (+)	Treatment (+) oPOM N (+) Bray-1 P (+)	oPOM N (+)	oPOM N (+) Bray-1 P (+)
Shoot C:N	Treatment (+) oPOM N (-) POXC (-) PMC (+) pH (+)	oPOM N (-) POXC (-) pH (+)	oPOM N (-)	Treatment (-) oPOM N (-) Bray-1 P (-)	oPOM N (-) Bray-1 P (-)	oPOM N (-)

2.4 Discussion

2.4.1 Functional trait contrasts between species

The three cover crop species in this study differentiated clearly by functional type; these functional contrasts can then inform understanding of species responses to growing conditions. While it is unsurprising that the N-fixing legume had higher leaf and root N and lower shoot and root C:N than the non-legumes, we also found important differences in less commonly studied cover crop traits. For instance, axis 2 of the trait PCA showed SLA in opposition to R:S, which may indicate a continuum of cover crop sensitivity to water availability. Species with lower SLA are typically more drought tolerant (Wright et al. 2005; Reich et al. 1999), and those with higher R:S can explore a greater volume of soil for water (Karcher et al. 2008; Wang et al. 2018). For rye and dwarf essex, lower SLA and higher R:S suggests their performance is less likely to be constrained by water availability, whereas high SLA and low R:S for clover could contribute to poor performance and competitive potential under water-limited conditions. Covariation between R:S and leaf and root P underscores the importance of root biomass for scavenging and retaining soil P. High leaf and root P for dwarf essex in particular suggests that brassicas with deep tap roots enhance soil P recycling, especially because brassicas tend to produce high biomass (Wagg et al. 2021; Grime 1998).

2.4.2 Patterns of trait variation within species

In addition to strong functional trait contrasts between species, we found support for our hypothesis that trait variation within species would be substantial. That intraspecific and interspecific variation contributed equally to total trait variation underscores the need for measuring both sources of variation in cover crop research. In natural communities, intraspecific trait variation can comprise one-quarter to one-third of total trait variation (Siefert et al. 2015), but artificial selection for use in annual cropping systems, combined with strong environmental and management gradients, can increase the relative importance of intraspecific variation (Martin et al. 2018; Roucou et al. 2018). The two traits for which intraspecific variation had the greatest relative importance – leaf P and R:S – directly influence agroecosystem nutrient scavenging, retention, and recycling (Wilke and Snapp 2008). Further, plasticity in whole-plant traits, which were most variable overall (Siefert et al. 2015), may be particularly consequential for agroecosystem function. Plant height and R:S are related to total productivity and biomass (Wagg et al. 2021), and many ecosystem services from cover crops scale directly with biomass, including N supply from BNF, nutrient retention, and weed suppression (Blesh, VanDusen, and Brainard 2019; Finney, White, and Kaye 2016; MacLaren et al. 2019). Variation in biomass allocation above- versus belowground can also impact soil C sequestration because root C inputs to soil are preferentially retained and a larger contributor to SOM than aboveground inputs (Rasse, Rumpel, and Dignac 2005; Puget and Drinkwater 2001; Austin et al. 2017).

2.4.3 Soil properties explain intraspecific trait variation

Our hypothesis that soil health indicators of nutrient cycling and availability would best explain cover crop trait variation was partially supported, with oPOM N and Bray-1 P occurring most frequently as significant predictors in regression models. However, there were also species-specific patterns. While dwarf essex traits responded primarily to oPOM N, and rye traits to oPOM N and Bray-1 P, clover traits had significant associations with oPOM N, Bray-1 P, pH, and POXC, suggesting that more diverse suite of indicators may be useful for predicting legume responses to soil health.

That clover root N, leaf P, and root P all increased, while root C:N decreased, with soil P is unsurprising given that legume growth is often P-, rather than N-limited (Vitousek et al. 2013; Isaac et al. 2011). As soil pH increased above the mean of 7.4 in our study, reduced availability of other nutrients required for BNF (e.g., iron, boron) may have also constrained legume performance, resulting in lower clover leaf N and R:S, and higher shoot C:N (Hartemink and Barrow 2023; Neina 2019; Vitousek et al. 2013). Higher leaf N and P, and lower shoot C:N for clover as oPOM N increased in both mixture and monocrop was unexpected given that rates of legume N fixation typically decrease with increasing soil N availability (Peoples et al. 2012; Blesh 2019). Rather than representing a response to nutrient availability, the relationships between clover traits and oPOM N could instead reflect trait variation in response to soil structure given that oPOM N is closely linked to aggregate stability (Drinkwater and Snapp 2022). Significant relationships between clover traits and POXC, another indicator associated with soil aggregation, also suggest that clover performance was influenced by soil structure (Culman et al. 2012; Hurisso et al. 2016). For instance, the 47% increase, and 34% decrease, in clover R:S associated with POXC and %clay, respectively, indicate that clover root growth was constrained in heavy clay soils, but increased pore space with higher POXC may have allowed for greater root growth. Increased growth belowground versus aboveground with increasing POXC is further reflected in the concomitant decrease in clover height with POXC.

Similar to clover, rye R:S decreased with %clay, which agrees with previous research demonstrating that growth of its fibrous root system is restricted in dense and compacted soil (Bukovsky-Reyes, Isaac, and Blesh 2019). Despite this constraint, there was a strong, positive relationship between rye R:S and Bray-1 P, and to a lesser extent oPOM N, suggesting root proliferation under nutrient-rich conditions for rye. In contrast, lower R:S for dwarf essex with increasing oPOM N indicates a shift in allocation from belowground to aboveground growth as nutrient availability increases (Qi et al. 2019). Given that dwarf essex trait variation was only measured in mixture, though, and thus represents the integrated effect of interspecific interactions and soil conditions, this relationship could alternatively reflect stronger competition with rye as soil N availability increases. Despite differential R:S responses to oPOM N, both rye and dwarf essex produced higher quality shoots and roots (i.e., lower C:N) as oPOM N increased, which can then influence rates of residue decomposition and N mineralization following cover crop termination (Thapa et al. 2022; Kuo and Sainju 1998).

Although increasing soil P availability had a beneficial association for several rye and clover traits, the lack of responsiveness of dwarf essex traits to soil P, combined with its high leaf and root P relative to the other species, suggests that it was a strong P scavenger. Brassica species like dwarf essex may therefore have potential for enhancing agroecosystem P cycling across a wide range of growing conditions (Akhtar, Oki, and Adachi 2009). Interestingly, dwarf essex had lower height and SLA with higher clay, possibly because clay soils have lower plant available water capacity, and both traits would be expected to decrease with reduced water availability. Relatedly, water availability may in part explain why SLA for all three species increased with oPOM N. Due to its associated with soil aggregation, oPOM N could, in turn, reflect improved soil water holding capacity, thus contributing to greater water availability and higher SLA (Wright et al. 2005; Reich et al. 1999). SLA can also increase with N fertilization (Knops and Reinhart 2000), providing another potential mechanism underlying the relationship between SLA and oPOM N given that POM fractions are likely an important nutrient source for cover crops (Blesh 2019; Bu et al. 2015).

2.4.4 Trait expression in mixture and monocrop

We found strong support for our hypothesis that interspecific interactions in mixture would induce trait plasticity, though the effect of planting treatment on trait variation was generally smaller than that of the soil gradient. Higher leaf P for rye in mixture relative to monocrop (Figure 2-5) suggests that niche complementarity and interspecific facilitation occurred in mixture, potentially due to increased P mobilization from legume rhizosphere acidification (Xue et al. 2016; Hinsinger et al. 2011). Similarly, the increase in leaf N, and decrease in shoot C:N, for rye in mixture indicates greater N availability from either niche differentiation or facilitation, or both, when combined with a legume (Blesh, VanDusen, and Brainard 2019; Izaurralde, McGill, and Juma 1992). Differences in rye leaf N and P responses to soil properties between mixture and monocrop provide additional insights into interaction dynamics. For instance, despite higher leaf P for rye in mixture overall, the positive relationship between rye leaf P and soil P in monocrop, but not mixture, suggests that dwarf essex posed competition for soil P in mixture (Table S2-9). This aligns well with other lines of evidence in this study indicating that dwarf essex is an excellent P scavenger, including its high leaf and root %P and strong performance across all levels of soil P availability. Strong competitive potential of dwarf essex for soil P may also explain why rye leaf N did not increase with Bray-1 P in mixture, but did in monocrop. Further, although rye leaf N decreased with increasing soil pH in monocrop, this negative effect of high pH disappeared in mixture, perhaps because legumes can contribute to rhizosphere acidification and increased nutrient availability in mixture.

In contrast to rye, clover leaf N and P were lower in mixture relative to monocrop. The decrease in leaf P could be driven by the non-legumes being superior competitors for soil P, despite a potential increase in overall P mobilization from the legume. Indeed, previous research has found that when legumes increase P availability, non-legume roots tend to proliferate into the

P-rich patches (Zhang et al. 2016). Although upregulation of legume N fixation is common in response to competition for soil N (Blesh 2019; Schipanski and Drinkwater 2011), lower leaf N for clover in mixture suggests that its performance was constrained overall when grown with rye and dwarf essex. Given that legume P uptake was likely constrained in mixture due to competition, this may have limited N fixation rates and reduced overall N concentrations. These negative competitive effects are further reflected in clover trait relationships with pH, where leaf N decreased, and shoot C:N increased, with pH in mixture, but not in monocrop, which is the opposite pattern from rye. While it is likely that clover increased nutrient availability in fields with high pH in both planting treatments, the degree of interspecific competition for solubilized nutrients in mixture was probably stronger than that of intraspecific competition in monocrop. A combination of competition for soil water and light likely reduced clover SLA and height in mixture relative to monocrop. Although clover SLA increased with soil health indicators linked to soil structure, including oPOM N and POXC (Drinkwater and Snapp 2022; Hurisso et al. 2016), and thus potentially water availability, the large root systems of rye and dwarf essex may have allowed them to outcompete clover for soil water. In turn, this could have resulted in lower SLA for clover in mixture to reduce transpiration and conserve water (Wellstein et al. 2017). Lower SLA could then limit photosynthetic capacity and growth, especially because legume N fixation is energetically costly (Vitousek et al. 2013), contributing to lower clover height in mixture.

2.4.5 Implications for agroecosystem function and management

Our study demonstrates that cover crop functional traits vary widely not only between species, but also within species in response to environmental and management conditions. Given that functional trait variation scales up to impact agroecosystem dynamics at higher levels of ecological organization (Wood et al. 2015), and that intraspecific variation comprised half of total trait variation in this study, we argue that refining understanding of trait variation both within and across species is critical for advancing the science and practice of cover cropping. For instance, while combining species with contrasting traits is a key strategy for enhancing multiple agroecosystem functions (Blesh 2018; Finney and Kaye 2017; Storkey et al. 2015), we found that functional contrasts also promoted interspecific interactions at the community level that altered trait expression within species. While trait variation for rye indicated that facilitation occurred, which could enhance ecosystem services from rye, there was also evidence that competitive interactions constrained legume performance and its N supply function (Blesh 2018; Crews et al. 2016). Examining the extent and direction of cover crop trait variation improves understanding of the drivers and outcomes of these interactions, which can help refine management for multiple benefits.

Intraspecific trait variation in response to soil conditions was substantial. This trait plasticity can then translate into significant effects on ecosystem functions and processes (Lavorel and Garnier 2002). Variation in shoot and root C:N, for example, has implications for the proportion of cover crop C sequestered in different organic matter fractions, with consequences for soil fertility and climate change mitigation (Zhang et al. 2022). Cover crop morphological and chemical traits also play a central role in supporting agroecosystem biogeochemical cycles, helping to retain and supply nutrients to farm fields, which reduces nutrient losses and the need for energy-intensive synthetic fertilizers (Tonitto, David, and Drinkwater 2006; Blesh and Drinkwater 2013).

Given that we found trait- and species-specific responses to soil conditions, this highlights the need for tailoring management based on goals and context (Damour, Navas, and

Garnier 2018). For example, although rye had the highest mean R:S and strong potential for retaining nutrients in high fertility soils, the large decrease in rye R:S with clay content could limit its success in fine-textured soils, making species with coarse taproots, like dwarf essex, a more promising option in those conditions (Bodner, Leitner, and Kaul 2014; Chen and Weil 2010). Furthermore, because rye and dwarf essex traits indicated strong competitive potential for soil P and water, whereas clover performance was likely constrained by those resources, mixture design should be adjusted based on soil health status (e.g., soil fertility and structure) to allow for success of each component species.

2.5 Conclusion

Results of our field experiment across 13 farm fields in Michigan demonstrate that intraspecific trait variation is just as substantial as interspecific. Trait variation within species was driven by complex biotic and abiotic interactions, with significant trait variation occurring both in response to the soil health gradient and to species interactions in mixture. As we had expected, soil health indicators linked to nutrient availability (i.e., oPOM N, soil P) were important for explaining trait variation, but soil structure also emerged as a potential driver of trait variation, especially for the legume and for traits sensitive to soil water availability. When grown together in mixture, we also found that contrasting and complementary characteristics between cover crop species can fuel interactions that induce trait plasticity, with implications for mixture composition and ecosystem services. Given the utility of our approach for elucidating potential mechanisms underlying cover crop outcomes, we call for more widespread use of trait-based approaches in cover crop research across a wide range of environmental conditions and management systems. Developing context-specific understanding of cover crop outcomes can then inform species selection, seeding rates, and mixture composition to meet environmental and management goals.

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2.7 Supplemental Material

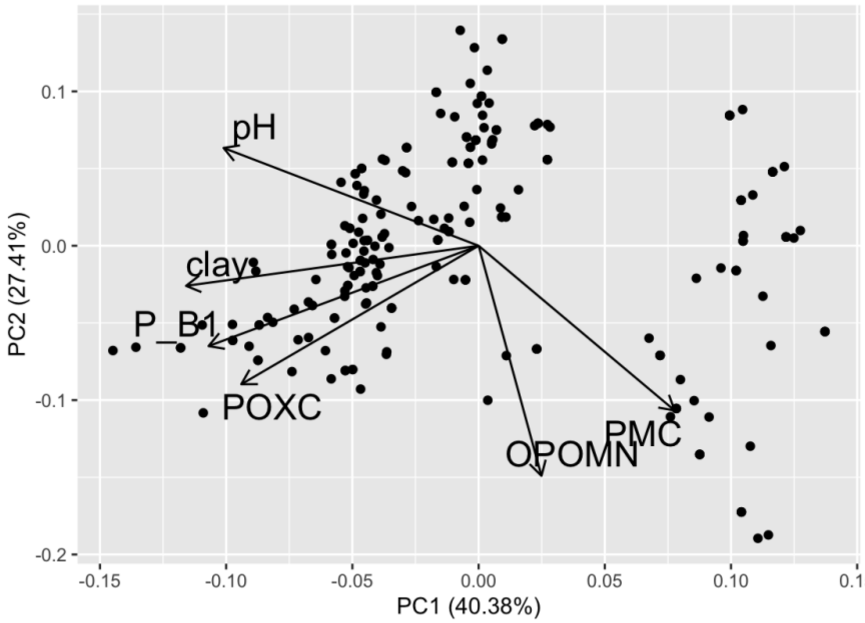

Figure 2-6: PCA of six soil health indicators included in regression analyses. P_B1 = Bray-1 P; POXC = permanganate oxidizable carbon; OPOMN = occluded particulate organic matter nitrogen; PMC = potentially mineralizable carbon.

Table 2-6: PCA loadings for soil health indicators.

Soil health indicator	**Component 1 (40.38%)**	**Component 2 (27.4%)**	**Component 3 (10.3%)**
oPOM N	0.11	-0.66	0.03
pH	-0.45	0.28	-0.47
Bray-1 P	-0.48	0.29	0.23
PMC	0.35	-0.48	-0.62
POXC	-0.42	-0.40	0.34
% clay	-0.52	-0.12	-0.48

Table 2-7: PCA loadings for cover crop functional traits.

Functional trait	**Component 1 (47.8%)**	**Component 2 (20.6%)**	**Component 3 (14.6%)**
Height	-0.39	0.03	-0.28
SLA	0.28	0.52	0.10
Shoot C:N	-0.38	0.20	0.18
Leaf N	0.45	-0.005	-0.06
Leaf P	0.17	-0.58	0.25
R:S	-0.05	-0.26	0.73
Root C:N	-0.42	-0.13	-0.18
Root N	0.45	0.09	-0.14
Root P	0.13	-0.51	-0.48

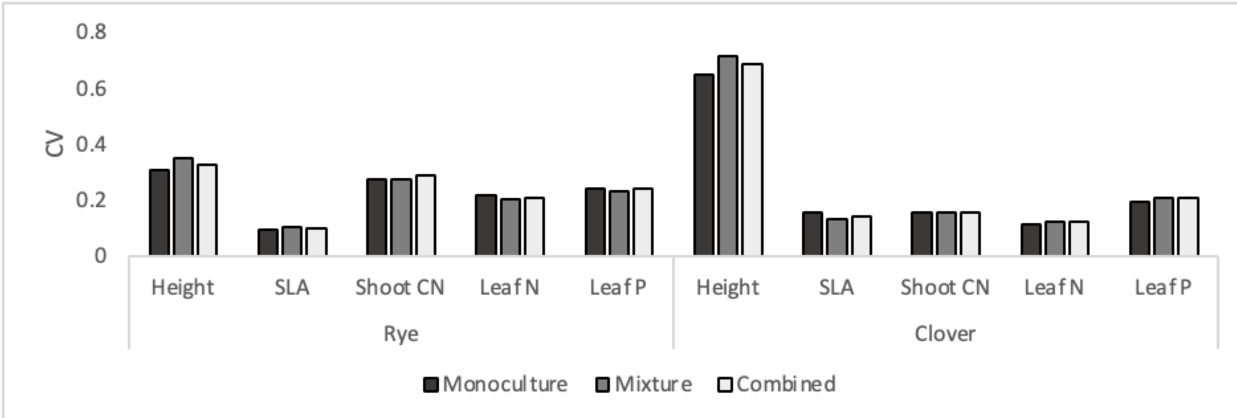

Figure 2-7: Magnitude of variation, shown here as the coefficient of variation (CV), for rye and clover aboveground functional traits in sole-planted (monoculture) versus mixture treatments, and combined across the two planting treatments. SLA = specific leaf area; shoot CN = shoot carbon:nitrogen.

Table 2-8: Regression models for clover aboveground traits in monocrop (top) and mixture (bottom). N=47 for all models. SLA = specific leaf area; Shoot C:N = shoot carbon to nitrogen ratio; PMN = potentially minerlizable nitrogen; PMC = potentially mineralizable carbon; POXC = permanganate oxidizable carbon; fPOMN = free particulate organic matter nitrogen; oPOMN = occluded particulate organic matter nitrogen; Marg. = Marginal; Cond. = Conditional.

MONOCROP	**Intercept**	**PMC**	**POXC**	**oPOMN**	**pH**	**Bray-1 P**	**%clay**	**Year**	**Marg. R^2**	**Cond. R^2**
log(Height)	3.04***	0.002	-0.0009**	0.0005	-0.125	0.0009	0.009	-1.01***	0.62	0.97
	(0.16)	(0.003)	(0.0003)	(0.003)	(0.126)	(0.0009)	(0.005)	(0.064)		
log(SLA)	5.85***	0.002	0.00001	0.004*	0.043	0.00008	-0.002	-0.214***	0.56	0.70
	(0.043)	(0.002)	(0.0002)	(0.001)	(0.048)	(0.0005)	(0.003)	(0.035)		
log(Leaf N)	1.52***	-0.0005	0.0001	0.004**	-0.072	-0.0001	-0.002	0.042	0.20	0.87
	(0.053)	(0.002)	(0.0001)	(0.001)	(0.051)	(0.0004)	(0.002)	(0.028)		
log(Leaf P+1)	0.308***	0.0006	-0.00003	0.0008*	0.008	0.0007***	0.0001*	0.079***	0.69	0.88
	(0.013)	(0.0005)	(0.00004)	(0.0004)	(0.014)	(0.0001)	(0.0006)	(0.009)		
log(Shoot C:N)	2.59***	0.003	-0.0001	-0.006**	0.121	-0.001	-0.0006	-0.052	0.32	0.82
	(0.066)	(0.002)	(0.0002)	(0.002)	(0.068)	(0.0006)	(0.003)	(0.04)		
MIXTURE	**Intercept**	**PMC**	**POXC**	**oPOMN**	**pH**	**Bray-1 P**	**%clay**	**Year**	**Marg. R^2**	**Cond. R^2**
log(Height)	2.82***	0.005	-0.0003	-0.004	-0.108	0.00006	-0.006	-1.12***	0.74	0.97
	(0.125)	(0.003)	(0.0002)	(0.002)	(0.114)	(0.0007)	(0.006)	(0.062)		
log(SLA)	5.77***	-0.001	0.0004**	0.003*	-0.059	-0.0005	-0.004	-0.047	0.33	0.68
	(0.05)	(0.002)	(0.0002)	(0.001)	(0.047)	(0.0004)	(0.003)	(0.038)		
log(Leaf N)	1.43***	-0.002	0.0005***	0.002**	-0.181***	-0.0004	-0.004	0.031	0.56	0.93
	(0.04)	(0.001)	(0.0001)	(0.0008)	(0.037)	(0.0003)	(0.002)	(0.023)		
log(Leaf P+1)	0.296***	-0.0001	-0.00001	0.001*	0.012	0.0005**	0.002	0.067***	0.54	0.80
	(0.016)	(0.0006)	(0.00005)	(0.0004)	(0.016)	(0.0002)	(0.001)	(0.013)		
log(Shoot C:N)	2.67***	0.002	-0.0005**	-0.004*	0.135*	-0.0004	0.004	-0.082	0.45	0.75
	(0.058)	(0.002)	(0.0002)	(0.002)	(0.059)	(0.0006)	(0.004)	(0.048)		

Table 2-9: Regression models for cereal rye aboveground traits in monocrop (top) and mixture (bottom). N=47 for all models except height in mixture, where N=46 due to an outlier. SLA = specific leaf area; Shoot C:N = shoot carbon to nitrogen ratio; PMN = potentially mineralizable nitrogen; PMC = potentially mineralizable carbon; POXC = permanganate oxidizable carbon; fPOMN = free particulate organic matter nitrogen; oPOMN = occluded particulate organic matter nitrogen; Marg. = Marginal; Cond. = Conditional.

MONOCROP	**Intercept**	**PMC**	**POXC**	**oPOMN**	**pH**	**Bray-1 P**	**%clay**	**Year**	**Marg. R^2**	**Cond. R^2**
log(Height)	3.42***	0.00003	-0.00006	-0.006**	-0.02	0.0006	0.013*	-0.045	0.13	0.93
	(0.14)	(0.003)	(0.0002)	(0.002)	(0.086)	(0.0006)	(0.005)	0.059		
log(SLA)	5.52***	-0.001	-0.0002	0.003**	-0.012	-0.001*	-0.001	-0.086	0.37	0.76
	(0.042)	(0.002)	(0.0002)	(0.001)	(0.035)	(0.0004)	(0.003)	(0.047)		
log(Leaf N)	1.16***	-0.005	0.0002	0.005**	-0.143*	0.002**	-0.008*	0.038	0.30	0.89
	(0.085)	(0.002)	(0.0002)	(0.002)	(0.067)	(0.0005)	(0.004)	(0.049)		
log(Leaf P+1)	0.38***	-0.0004	0.00006	0.001*	-0.018	0.0007**	-0.0004	0.058**	0.28	0.81
	(0.03)	(0.001)	(0.00008)	(0.0007)	(0.026)	(0.0002)	(0.002)	(0.021)		
log(Shoot C:N)	3.05***	0.002	-0.0002	-0.006*	0.077	-0.003**	0.01	-0.092	0.22	0.82
	(0.129)	(0.004)	(0.0003)	(0.003)	(0.108)	(0.001)	(0.007)	(0.084)		
MIXTURE	**Intercept**	**PMC**	**POXC**	**oPOMN**	**pH**	**Bray-1 P**	**%clay**	**Year**	**Marg. R^2**	**Cond. R^2**
log(Height)	3.42***	0.001	-0.0005	-0.008**	-0.04	0.0007	0.008	-0.152	0.21	0.87
	(0.127)	(0.004)	(0.0003)	(0.003)	(0.119)	(0.0009)	(0.007)	0.075		
log(SLA)	5.52***	0.0004	-0.0001	0.005***	-0.033	0.0005	-0.004	-0.08	0.46	0.72
	(0.038)	(0.002)	(0.0001)	(0.002)	(0.039)	(0.0004)	(0.003)	(0.032)		
log(Leaf N)	1.34***	-0.0003	-0.00002	0.009***	0.0002	0.0009	-0.004	-0.078	0.25	0.92
	(0.092)	(0.002)	(0.0002)	(0.002)	(0.080)	(0.0006)	(0.004)	(0.047)		
log(Leaf P+1)	0.508	-0.002	0.00009	0.004***	0.031	0.0005	-0.002	0.019	0.35	0.81
	(0.037)	(0.001)	(0.0001)	(0.0009)	(0.037)	(0.0003)	(0.002)	(0.026)		
log(Shoot C:N)	2.75***	0.007	0.00004	-0.015***	0.034	-0.002	-0.013	-0.026	0.36	0.78
	(0.123)	(0.005)	(0.0004)	(0.003)	(0.125)	(0.001)	(0.008)	(0.095)		

Chapter 3 – Citizen Science Reveals Opportunities for Improving Sustainability Outcomes of Cover Crops[2]

Abstract

Cover crops can support numerous ecosystem services, including nutrient supply and retention, weed suppression, and carbon sequestration, many of which scale directly with cover crop biomass. However, there is a crucial need to identify strategies for optimizing management for maximum cover crop growth and benefits under real world conditions. We partnered with farmers in the U.S. Great Lakes region to quantify variation in cover crop performance across 253 fields on working farms, and to determine key drivers of variation. Cover crop performance was highly variable across fields. On average, multi-species mixtures accumulated twice as much biomass and nitrogen as cereal rye, the most popular cover crop in the region. Strong mixture performance was driven by a synergistic relationship between increases in both primary crop and cover crop diversity in rotations. Regression trees indicated that mixtures with higher species richness performed best, suggesting that higher richness offers "insurance" across heterogeneous environmental conditions such as weather and soil textures. Performance of mixtures with lower species richness was constrained by precipitation, unless fields had a history of organic soil amendment applications. Rye performance increased with growing degree days, underscoring the importance of practices that extend the rye growing season. We also found that interactions between management history and environmental conditions affected outcomes of other cover crop management decisions, such as planting method. These findings demonstrate a key role for

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increasing plant diversity in optimizing cover crop outcomes on working farms, and also highlight important synergies and positive feedbacks when using multiple ecological management practices. Our farmer-based citizen science approach is a promising tool for monitoring cover crop performance and identifying practical and context-specific opportunities for improving management to enhance agroecosystem function.

3.1 Introduction

Cover crops are gaining traction as a promising strategy for improving agricultural sustainability and resilience. Because cover crops are planted in windows between primary crops in rotation, they can be a feasible and highly effective tool for supporting critical ecosystem services across a variety of farming systems. For instance, several decades of research demonstrate their potential for sequestering carbon and building soil health (Drinkwater et al., 1998; McClelland et al., 2021) reducing nutrient pollution to surrounding waters (Tonitto et al., 2006), and controlling weeds and pests (Blesh et al., 2019). Many of these benefits scale directly with cover crop biomass (McClelland et al., 2021; Blesh, 2018; Finney et al., 2016; King and Blesh, 2018; MacLaren et al., 2019), such that realizing sustainability goals with cover crops hinges upon successful cover crop growth. That said, there are wide disparities in cover crop performance within and across regions and continents, presenting a critical need to identify strategies for optimizing management to maximize cover crop growth and benefits.

Existing approaches for studying cover crop performance on working farms excel in either breadth or depth, but not both. For instance, remote sensing approaches provide breadth by enabling large-scale cover crop analyses (Deines et al., 2023; Seifert et al., 2018), and have confirmed that cover crop biomass and ecosystem services are variable across farms (Hively et al., 2009), but often lack the resolution and accuracy to detect critical factors influencing cover crop outcomes (e.g., species composition, field management histories). On-farm experiments provide depth by capturing greater environmental and management detail to identify drivers of cover crop performance (e.g., Baraibar et al., 2020; Brooker et al., 2020; Florence et al., 2019; Reiss and Drinkwater, 2020), but are limited in scale by resource requirements. We currently lack a sufficiently refined approach to understanding the extent and drivers of variation in cover crop performance on real farms at spatial scales relevant to conservation program goals (e.g., watershed, regional, or national) and encompassing the broad range of factors affecting cover crop performance.

To address this need, we developed a novel citizen science approach that allows for collecting data with both breadth and depth (Billaud et al., 2021). By combining a management survey and field assessment performed by partnering farmers, we evaluated cover crop performance across 253 fields spanning 102 farms in six Great Lakes states between spring 2022 and 2023 (Figure 3-1, Table S3-4). The Great Lakes USA is one of the nation's most important agricultural regions due to its fertile soils and freshwater resources, especially within the context of climate change. However, unsustainable practices harm these soil and water resources. Harmful algal blooms in Lake Erie driven largely by nutrient losses from agricultural fields drew national attention in 2014 (Smith et al., 2015), which motivated concerted efforts in the region to increase cover crop adoption. Cover crops that overwinter are particularly important for addressing nutrient losses because they assimilate and retain nutrients as snow melts and soils thaw in the spring.

Cereal rye (*Secale cereale*) is the most popular cover crop in the region due to its cold-tolerance (CTIC-SARE-ASTA, 2023), making it a more reliable option for simplified row crop systems where the primary window for establishment is late fall following corn or soybean harvest. However, cover crop mixtures containing two or more species are also increasingly common (CTIC-SARE-ASTA, 2023). This stems in part from research demonstrating that increasing cover crop diversity can enhance overall productivity (Bybee-Finley et al., 2016; Kharel et al., 2023; Sainju et al., 2005), support a broader suite of ecosystem services (Blesh, 2018; Finney and Kaye, 2017), and improve plant community resilience (Kahmen et al., 2005; Tilman, 1996; Wendling et al., 2019). Mixtures can be more challenging to manage than cereal rye, and it remains unclear how successfully farmers are using them in practice.

Here we seek to: 1) quantify variation in overwintering cover crop biomass across farm fields; 2) identify key drivers of variation; and 3) determine whether trends differ between cereal rye and mixtures, which comprised 108 and 118 of the fields in our study, respectively. We combined a management survey and field assessment performed by partnering farmers to assess the extent and drivers of variation in cover crop performance. We summarized field management history data using five indicators that we integrated into an "ecological management index" or EMI. Our EMI encompasses three main dimensions of agroecosystem management – agro-biodiversity, low soil disturbance, and relative reliance on organic soil amendments - which places fields along a continuum from more conventional to more diversified management based on ecological principles (Kremen and Miles, 2012).

An ecological approach to management can enhance agroecosystem functions that, over time, have feedbacks on ecosystem services from cover crops, such as water infiltration and retention and soil nutrient availability (Zimnicki et al., 2020; Blesh, 2019). Because nutrient retention is a main service of interest from cereal rye, we also determined the proportion of rye fields reaching at least 1.0 Mg ha^{-1} of rye biomass, which was identified in previous research as a critical threshold for minimizing soil nitrate losses (Hively et al., 2009). We also measured nitrogen (N) assimilated in aboveground cover crop biomass across all rye and mixture fields as an indicator of N supply and recycling potential. Finally, we identified key factors influencing cover crop performance with regression tree analysis.

We hypothesize that, on average, cereal rye and mixture fields will produce similar levels of biomass, but that mixture biomass will be more variable due to greater management complexity despite potential for enhanced performance with higher species diversity. Additionally, we hypothesize that the main factors explaining variation in cover crop performance will differ between the two cover crop types due to differences in plant species and community responses to growing conditions, in part because they may be grown in distinct niches. For instance, mixtures are commonly planted following small grain harvest in late summer, whereas cereal rye is often used following corn or soybean harvest in late fall.

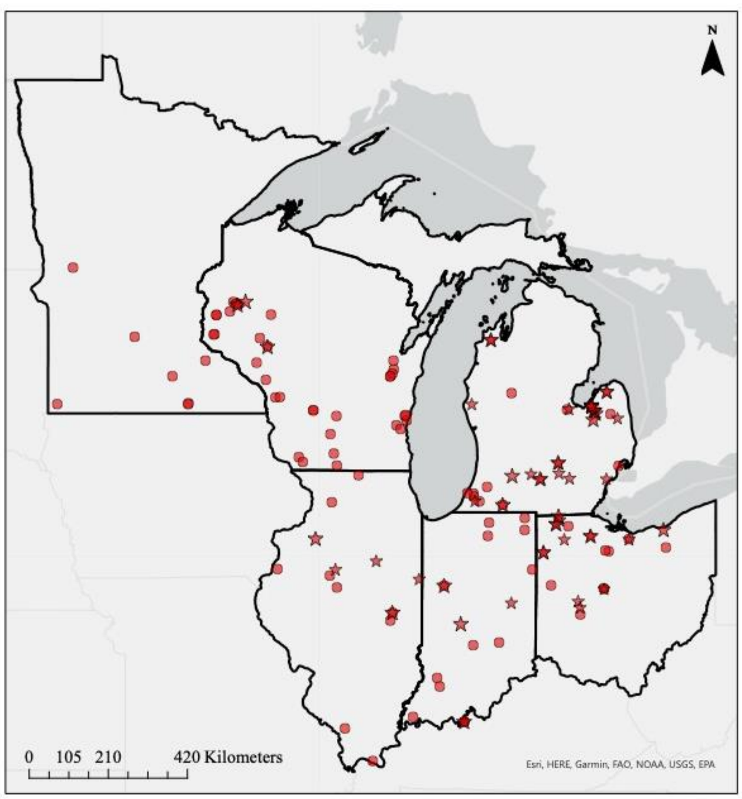

Figure 3-1: Farm locations. Stars denote farms that were visited for destructive biomass sampling to validate the citizen science approach.

3.2 Materials & Methods

3.2.1 Participant recruitment

Participation in this study was voluntary, and open to any farmer currently using cover crops in MI, OH, IN, IL, WI, or MN. We recruited participants through farmer email lists, networking at farmer-focused events, and through connections with conservation professionals, extension educators, and other agricultural stakeholders. Enrolled fields ranged from 0.01-93.1 ha, with a mean of 15.0 ha (Figure S3-4). In return for participating, each farmer received a personalized report including cover crop biomass and N assimilation estimates for their field(s) relative to others in the study, along with a small monetary incentive. Feedback from farmers indicated the report was a valuable study component.

3.2.2 Study design

For our citizen science approach, we used a field assessment and management survey to quantify variation in cover crop biomass across the region and identify key factors driving that variation. The USA Great Lakes region has a temperate climate, though substantial variation in temperature and precipitation can occur within the region during the cover crop growing season, particularly from northern to southern locations (US Department of Commerce, 2023). For instance, mean maximum temperatures for October ranged from 15.8°C in the northern portion of Michigan's lower peninsula to 20.7°C in southern Indiana in 2021, and from 12.9°C to 19.7°C in 2022. Spring temperatures followed similar trends, with mean maximum temperatures of 20.4°C in northern Michigan and 24.1°C in southern Indiana in May 2022, and of 19.7°C and 22.8°C in May 2023. Trends for precipitation varied even more across the region and study years. In northern Michigan, total precipitation in October 2021 and 2022 was 3.9 cm and 9.5

cm, respectively, while in May 2022 and 2023 it was 2.7 cm and 5.2 cm. Southern Indiana showed more variation in precipitation, with very wet weather in the first study year – 14.1 cm in October 2021 and 17.2 cm in May 2022 – and drier conditions in the second study year - 4.9 cm in October 2022 and 7.2 cm in May 2023. The diversity of weather conditions, soil types, and farming systems in this region make it an ideal location for testing how different factors influence cover crop outcomes.

3.2.2.1 Field assessment

Cover crop biomass was the main response variable in this study, and was estimated using a rapid and low-cost field assessment protocol performed by participating farmers. The field assessment builds on previous studies showing that plant height and percent ground cover are strongly correlated with cover crop biomass (Brennan and Smith, 2023; Prabhakara et al., 2015; Xia et al., 2021). Shortly before termination, participants were instructed to visit their fields to collect cover crop height measurements, ground cover photos, and weed pressure rankings. In the first third of the field, they selected a location with representative cover crop biomass (i.e., avoiding areas with unusually low or high biomass) and collected three plant height measurements per species, for up to the four most dominant species in the case of mixtures. They then took a ground cover photo by extending an arm out perpendicular to the body and parallel to the ground, avoiding capturing shadows or other objects in the photo. Using a Likert scale, they rated the weed pressure at that location (1 = very low weed pressure, 5 = very high). Finally, if sampling a mixture, they also reported visual estimates of the proportions of the most dominant species for up to four species. They then repeated these steps at a location closer to the center of the field, and then at a location in the last third of the field. These data were reported using a Qualtrics survey that walked participants through the protocol step by step and took an average of 30 minutes to complete per field. Hardcopy datasheets were available upon request (Appendix A). To ensure data quality and consistency, participants viewed a short demonstration video prior to performing the field assessment. Following data collection, we processed the ground cover photos in Foliage (Patrignani, 2020), a batch-processing application that calculates the percentage of ground cover in photos. We then used the field assessment data to calculate *%Cover x Height* for each field, with heights weighted by species for mixtures based on the visual proportion estimates, and with a correction factor applied based on the weed pressure ratings to account for weeds in the cover crop biomass estimates. Specifically, weed pressure ratings of 5, 4, 3, and 2 corresponded with correction factors of 0.2, 0.4, 0.6, and 0.8, while a rating of 1 (i.e., very low weed pressure) received no correction factor.

3.2.2.2 Validation of field assessment

To validate the field assessment approach, we visited a subset of farms during spring 2022 and 2023 (Figure 3-1) to collect biomass samples using a traditional destructive sampling technique. In each field, we selected three sampling locations following the same approach described above. At each location, we collected aboveground biomass from a 0.25 m^2 quadrat, separating by species for mixtures and grouping weeds into one pool. Samples were dried at 60°C for 48 hr and weighed. We then fit regression models between observed biomass (destructively sampled) and predicted biomass (field assessment) and determined that the field assessment accurately predicted cover crop biomass for both cereal rye (R^2=0.84, N=55) and mixture fields (R^2=0.79, N=38) (Figure S3-5). These regression relationships were then used to convert the field assessment data for all remaining fields into biomass estimates in kg ha^{-1}.

3.2.2.3 Nitrogen analysis

For fields that we visited to destructively sample aboveground biomass, we coarsely ground the dried biomass samples (<2 mm) using a Wiley mill and then analyzed them for N concentration (%N) by dry combustion on a TruMac CN Analyzer (Leco Corp., St. Joseph, MI). We multiplied cover crop biomass by %N to calculate total N assimilated in cover crop biomass for each of those fields, summing across species for mixtures. The %N data were then averaged at the species level (Table S3-5) and used to quantify N assimilation for all remaining fields based on the corresponding species data and biomass estimates from the field assessment. Cereal rye fields showed wide variation in growth stage, which can influence %N; we therefore reviewed the ground cover photos submitted for each rye field and assigned a %N value based on whether the plants were at an early, intermediate, or advanced growth stage. We used the mean of the five highest and lowest %N values from our rye biomass samples for early and advanced growth stages (4.63% and 1.34%, respectively), and the mean %N from Table S3-5 for intermediate growth stages (2.81%). For mixtures, we multiplied species-level biomass (estimated based on the species proportion data reported in the field assessment) by the corresponding %N before summing across all species for total mixture N assimilation.

3.2.2.4 Management survey

Participating farmers completed an online management survey via Qualtrics (Appendix B). The survey asked questions about how they managed their cover crop that season, and about their management history more broadly. Table 3-1 summarizes key variables collected in the management survey. Cover crop species richness and functional diversity were calculated based on the species each farmer reported planting, rather than on species emergence. Precipitation and GDD during the cover crop season were both calculated using the Nutrien eKonomics GDD and

Table 3-1: Description of explanatory variables included in regression tree models.

Variable	Description
Cover crop (CC) management	
CC type	Type of CC - cereal rye or mixture.
Seeding rate	Cover crop seeding rate (kg ha^{-1}).
Richness	Number of overwintering cover crop species.
Functional diversity	Number of overwintering cover crop functional groups; each cover crop functional group (grass, legume, brassica, or non-legume broadleaf) received one point, with morphological complementarity (e.g., rye + vetch) awarded one additional point. Ranges from 1-5.
Planting method	Drilled, broadcast, broadcast plus incorporation, or aerial seeded.
CC N	N fertilizer applied during the cover crop growing season (kg ha^{-1}).
CC P	P fertilizer applied during the cover crop growing season (kg ha^{-1}).
CC Manure	Manure applied during the cover crop growing season (tons ha^{-1}).
CC Compost	Compost applied during the cover crop growing season (tons ha^{-1}).
Preceding crop	Crop grown immediately preceding the cover crop.
PC N	N fertilizer applied to the preceding crop (kg ha^{-1}).
PC P	P fertilizer applied to the preceding crop (kg ha^{-1}).
PC Manure	Manure applied to the preceding crop (tons ha^{-1}).
PC Compost	Compost applied to the preceding crop (tons ha^{-1}).
General management history	
Ecological Management Index (EMI)	Sum of normalized rotational diversity, cover crop diversity, years of cover crop use, soil disturbance, and organic amendment scores. Ranges from 0-5, with higher scores indicative of management based on ecological principles.
Rotational diversity	Based on reported cash crop rotation from the prior five years. Each annual crop species received one point, while perennials received two points. Normalized to a scale of 0-1.
Cover crop diversity	Based on diversity of cover crop functional types (grass, legume, and brassica). Each functional type received a numeric score based on categorical responses to the frequency with which they appeared in the field: Never = 0; This is my first year = 1; Less than every few years = 2; Every few years = 3; Every other year = 4; Every year = 5. For each field, scores were summed across the three functional types and normalized to a scale of 0-1.
Years of cover crop use	Number of years the field has been planted to a cover crop, reported categorically (1; 2 to 5; 6 to 10; 11 to 20; 20+) then converted to numeric scores and normalized to a scale of 0-1.
Low soil disturbance	Indicator of soil disturbance based on tillage practices, reported categorically (no-till; reduced tillage; conventional tillage) for each of the prior five years and for the dominant historical tillage regime. The prior five years were scored individually as no-till = 3, reduced tillage = 2, or conventional tillage = 1, then summed across the five years and multiplied by a factor of 1, 2 or 3 based on historical tillage (conventional, reduced, or no-till, respectively). Scores for each field were then normalized to a scale of 0-1.
Organic amendments	Frequency of manure and compost applications, reported categorically for each amendment type (multiple times a year; once a year; every other year; every few years; never) then converted to numeric scores, summed across the two amendment types, and normalized to a scale of 0-1.
Environmental factors	
Soil texture	Reported categorically as clay, clay loam, sand, sandy loam, silt loam, loam or other.
Topography	Reported categorically as mostly flat, gentle slopes (2-6%), moderate slopes (6-12%), or steep slopes (> 12%).

GDD	Cover crop growing degree days using a base temperature of 0°C, based on reported planting and sampling dates for each field.
Precipitation	Total rainfall during the cover crop growing season (cm) based on reported planting and sampling dates for each field.

Rainfall Tracker tools, which use publicly available weather station data to generate location-specific estimates based on the reported planting and sampling dates (Nutrien eKonomics, 2023). To protect farmer privacy, we collected field location data at the US Postal Service zip-code scale; the weather data are thus also at the zip-code scale.

Drawing on the management history data reported by farmers, the EMI is comprised of five indicators, including rotational diversity, cover crop diversity, years of cover crop use, low soil disturbance, and use of organic amendments, each calculated as described in Table 3-1. Rotational diversity was based on species richness of the cash crops in rotation, with annuals receiving one point, and perennials receiving two due to their known benefits for soil health and agroecosystem function (King and Blesh, 2018; Sprunger et al., 2020; Rakkar et al., 2023). For instance, a corn-soy rotation would receive a score of 2, while a corn-soy-alfalfa rotation would receive a score of 4. For cover crop diversity, participants reported how frequently they used each of three cover crop functional types – legumes, grasses, and brassicas – which was then used to create a functional diversity-based score, ranging from 1 to 15. A field planted to cereal rye every year would receive a score of 5, for example, but a field planted to a functionally diverse mixture every year would receive the maximum score of 15. First-time cover crop users participating in the study who planted cereal rye would receive a score of 1, while those who planted a mixture as their first cover crop would score between 1-3 depending on the functional diversity of the mixture. Years of cover crop use for each field was based on the number of years cover crops were actually planted in the field, rather than simply the number of years since the farmer had first started using cover crops in the field because cover crops may not have been planted in every year. Soil disturbance was quantified based on both recent tillage history (previous five years) and long-term tillage history (general tillage practices prior to the previous five years), with scores ranging from 5 to 45. Fields managed with conventional practices over the past five years would receive an initial score of 5, and would be multiplied by a factor of one, two, or three if managed using conventional, reduced tillage, or no-till prior to the previous five years, respectively, resulting in scores of 5, 10, or 15. A field with both a short- and long-term history of no-till would receive the maximum score of 45. Finally, for use of organic amendments, participants reported how frequently they applied manure and compost to their field, with “never” for either amendment corresponding to a minimum score of 0, and “multiple times a year” for both manure and compost corresponding to a maximum score of 8. Scores for each of the five indicators were normalized prior to summing to calculate the overall EMI for each field.

3.2.3 Statistical analysis

All statistical analyses were performed in R Statistical software (R Foundation for Statistical Computing, 2024). All data processing steps for management survey variables prior to analysis are described in Table 3-1. We first used descriptive statistics, including means, ranges, and coefficients of variation (CV) to explore trends in the data. To determine the most important factors influencing cover crop performance, we then conducted regression tree analyses using the rpart v4.1.23 and rpart.plot v3.1.1 packages in R (Therneau et al., 2023; Milborrow, 2022). Regression tree analysis is well suited to this type of research because it produces easily interpretable and management-relevant results. Using a top-down approach, the dataset is divided into subgroups (branches) based on the explanatory variables that explain the most heterogeneity in the response variable. The expected value for each subgroup is represented by the node (leaf) at the end of each branch. This analysis is considered robust against multicollinearity, allowing for the full set of explanatory variables to be included in the models, and is generally not sensitive to scale such that those variables may be included in their original units, improving interpretability. It is also appropriate for non-normally distributed data as was the case here, and well as for datasets containing both continuous and categorical independent variables. Finally, regression tree analysis can handle missing values because it proceeds by performing splits based on available data, which is useful here because some participants skipped survey questions (8.9% of respondents).

We generated three regression trees - one for all rye and mixture fields combined, and then for each cover crop type independently. We included all variables in Table 3-1 in each of the trees, with a few exceptions: the "CC type" variable was only included in the combined tree; only the rye tree contained the seeding rate variable; and species richness and functional diversity indices were excluded from the rye tree because all rye fields would correspond to a value of 1. The trees were pruned using a cost-complexity approach to avoid overfitting, where 90% of the datapoints were used as the training dataset and the remaining 10% as the testing dataset to identify an optimal complexity parameter (cp) value. The rpart package automatically performs cross-validation ten times, but because the datapoints in the training and testing datasets are randomly determined each time a tree is generated, the cp value can change, though the overall structure of the tree typically remains the same. Given this, we manually repeated this cross-validation procedure 15 times for each tree and selected the most frequently occurring cp value for the final tree. We also selected a minimum terminal node value of ten samples per leaf.

3.3 Results

3.3.1 Characterization of cover cropped fields

The 226 cereal rye and mixture fields in this study spanned a diverse range of environmental and management characteristics (Tables 3-2 and 3-3). 84% of fields were either mostly flat or had gentle slopes. There was relatively even representation of sandy loam, silt loam, and clay loam soil textures in the dataset, with loam soils representing a slightly smaller proportion of fields, followed by clay and sand. Based on reported management histories, most fields trended towards conventional management, with a mean EMI of 1.78 (±0.67) on a scale of 0-5, with higher scores indicating ecological management approaches. However, there were notable differences across the individual EMI indicators. Low soil disturbance was one of the highest scoring components overall, reflecting that many fields were managed using reduced or no-till practices. On the other hand, use of organic amendments was highly variable and the lowest scoring component. Overall, mixture fields had a slightly higher mean EMI score than those in rye (1.87 ±0.66 versus 1.68 ±0.66, respectively), which was driven by three indicators: rotational diversity, cover crop diversity, and years of cover crop use.

The proportion of fields planted following small grain crops (e.g., winter wheat) was nearly four times higher for mixtures than for cereal rye, with over 80% of rye fields occurring after corn or soy compared to only 48% of mixtures. Consequently, cover crop mixtures had nearly twice as many growing degree days (GDD) and 23% more precipitation than cereal rye fields, on average. Nutrient inputs during the cover crop growing season were relatively uncommon (29% of all fields). Both cover crop types had similar planting method distributions, with drilling being most common.

3.3.2 Variation in cover crop performance

We found that cover crop biomass varied tremendously, ranging from 0 Mg ha^{-1} on several fields to 12.0 Mg ha^{-1} on the best performing field (Figure 3-2). While the overall range in mixture biomass was two-fold greater than that of cereal rye (0-12.0 Mg ha^{-1} vs. 0-6.4 Mg ha^{-1}), rye and mixtures had similar relative variability overall (CV = 1.16 and 1.15, respectively). Mean mixture biomass was also nearly two-fold higher than cereal rye biomass in both years. Cold and wet weather in the first year contributed to lower mean biomass for both cover crop types compared to the second year. Trends for shoot N assimilation reflected those of biomass. Mixtures contained an average of 39.7 (±42.4) and 58.4 (±62.9) kg N ha^{-1} in 2022 and 2023,

Table 3-2: Summary statistics for continuous explanatory variables for all cereal rye and mixture fields combined and by each cover crop type. CV = coefficient of variation.

Variable	*Mean*	*Range*	*CV (%)*	*N*
ALL				*226*
GDD	1509	222-4177	56.9	225
Precipitation (cm)	52.7	19.0-93.9	31.0	225
Richness	2.16	1-9	74.7	224
Functional diversity	1.79	1-5	58.1	225
EMI	1.78	0.2-3.2	37.4	205
Rotational diversity	0.32	0-1	58.1	213
Cover crop diversity	0.49	0-0.9	54.6	208
Years of cover crop use	0.34	0-1	79.3	214
Low soil disturbance	0.49	0-1	80.0	214
Organic amendments	0.14	0-0.8	1.1	205
CEREAL RYE				108
GDD	1096	222-4001	63.3	108
Precipitation (cm)	47.1	19.0-93.9	31.7	108
Seeding rate (kg ha^{-1})	79.7	16.8-201.8	39.6	106
EMI	1.68	0.20-2.95	39.2	99
Rotational diversity	0.30	0-1	50.6	104
Cover crop diversity	0.40	0-0.80	58.5	102
Years of cover crop use	0.31	0-1	81.0	104
Low soil disturbance	0.51	0-1	75.5	104
Organic amendments	0.14	0-0.44	92.9	99
MIXTURE				118
GDD	1886	432-4177	43.5	117
Precipitation (cm)	57.9	25.1-93.9	27.5	117
Richness	3.23	1-9	50.0	116
Functional diversity	2.51	1-5	39.3	117
EMI	1.87	0.20-3.19	35.3	106
Rotational diversity	0.34	0-1	62.5	109
Cover crop diversity	0.58	0-0.93	47.0	106
Years of cover crop use	0.36	0-1	77.5	110
Low soil disturbance	0.46	0-1	84.8	110
Organic amendments	0.14	0-0.78	117.1	106

Table 3-3: Proportion of fields in different groups for each categorical explanatory variable, for each cover crop type and all fields combined. PC = preceding crop; CC = cover crop.

Variable	**Proportion of Fields (%)**		
	All	*Cereal rye*	*Mixture*
Soil texture	*N = 226*	*N = 108*	*N = 118*
Sand	4.0	2.8	5.1
Clay	9.7	5.6	13.6
Loam	15.5	14.8	16.1
Sandy loam	25.7	30.6	21.2
Silt loam	21.2	20.4	22.0
Clay loam	23.5	25.0	22.0
Topography	*N = 217*	*N = 105*	*N = 112*
Mostly flat	41.9	38.1	45.5
Gentle slopes	42.4	41.0	43.8
Moderate slopes	14.7	20.0	9.8
Steep slopes	0.01	1.9	0.0
Preceding crop	*N = 225*	*N = 107*	*N = 118*
Corn	35.1	49.1	22.9
Soy	28.0	31.5	24.6
Small grain	29.8	12.0	45.8
Other	7.1	7.4	6.7
PC nutrient inputs⁺	*N = 212*	*N = 103*	*N = 109*
N fertilizer	52.4	56.3	48.6
P fertilizer	34.4	36.9	32.1
Manure	25.0	30.3	18.3
Compost	4.2	1.9	6.4
None	26.4	25.2	27.5
CC nutrient inputs⁺	*N = 226*	*N = 108*	*N = 118*
N fertilizer	4.4	7.4	1.7
P fertilizer	8.8	11.1	6.8
Manure	17.6	14.8	20.3
Compost	4.4	0.1	7.6
None	71.2	74.1	74.3
Planting method	*N = 226*	*N = 108*	*N = 118*
Drilled	67.7	63.0	72.9
Aerial	8.4	10.2	6.8
Broadcast	17.7	20.4	15.3
Broadcast + incorporate	5.8	6.5	5.1

respectively, compared to 17.6 (±19.8) and 29.7 (±26.6) kg N ha^{-1} for cereal rye. Additionally, only 32% of rye fields met the 1.0 Mg ha^{-1} biomass threshold for minimizing soil nitrate losses.

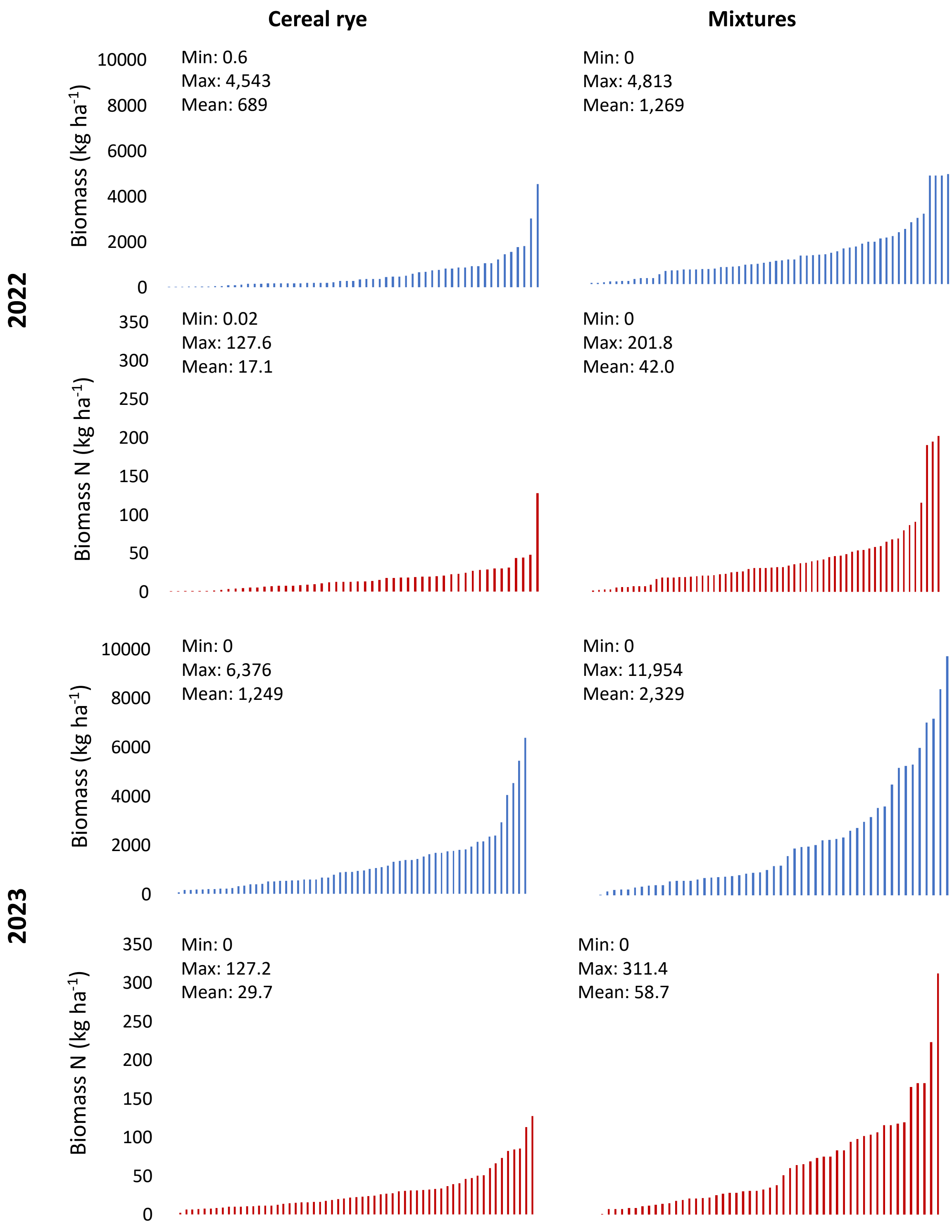

Figure 3-2: Left: Aboveground cover crop biomass and nitrogen (N) assimilation across cereal rye fields in 2022 (N=47) and 2023 (N=61). Right: Aboveground cover crop biomass and N across mixture fields in 2022 (N=64) and 2023 (N=54).

3.3.3 Key drivers of variation

Across all rye and mixture fields, the most important factor explaining cover crop biomass was the number of cover crop species (Figure 3-3a). Mixtures with five or more overwintering species were associated with the greatest mean biomass (3.9 Mg ha^{-1}), while mean biomass for cover crops with fewer than five species, including lower diversity mixtures and all rye fields, ranged from 0.5 to 2.7 Mg ha^{-1} depending on interactions between environmental and management conditions. Specifically, lower diversity cover crops with <873 GDD produced the least biomass, while for fields with >873 GDD, the next most important factor was the organic amendment score. Higher organic amendment scores (>0.17) were associated with greater biomass, particularly in loam and silt loam soils (2.7 Mg ha^{-1}). Fields with lower organic amendment scores still produced significant biomass – 2.2 Mg ha^{-1}, on average – if they received ample precipitation (>62 cm). However, fields with low organic amendment scores and low precipitation generally had poor performance. Under those conditions, drilling and broadcast seeding showed modest benefits over aerial seeding, especially in 2023.

In the analysis by cover crop type, regression trees were able to explain nearly one-third of regional variation in cereal rye and mixture biomass with just two and three variables, respectively. The regression tree for cereal rye included two splits – GDD and soil texture (Figure 3-3b). Rye biomass increased with GDD such that mean biomass in fields with >873 GDD was roughly three-fold higher than in those with <873 GDD (1.4 Mg ha^{-1} and 0.5 Mg ha^{-1}, respectively). For fields with >873 GDD, rye biomass was maximized when grown in loam, clay loam, or silt loam soils. The regression tree for mixtures on the other hand contained three splits – richness, precipitation, and the organic amendment score (Figure 3-3c). Similar to the regression tree for all fields, mixtures with five or more overwintering species performed best

(3.9 Mg ha^{-1}, on average), while biomass for mixtures with fewer than five species depended on precipitation. Lower diversity mixtures that received at least 74 cm precipitation produced over two times more biomass, on average, compared to those with less precipitation (2.5 Mg ha^{-1} and 1.2 Mg ha^{-1}, respectively). Importantly, regular use of organic amendments helped buffer against low precipitation, such that fields with higher organic amendment scores had more than double the mean biomass of fields with lower amendment scores when precipitation was limiting (2.0 kg ha^{-1} and 0.9 Mg ha^{-1}, respectively).

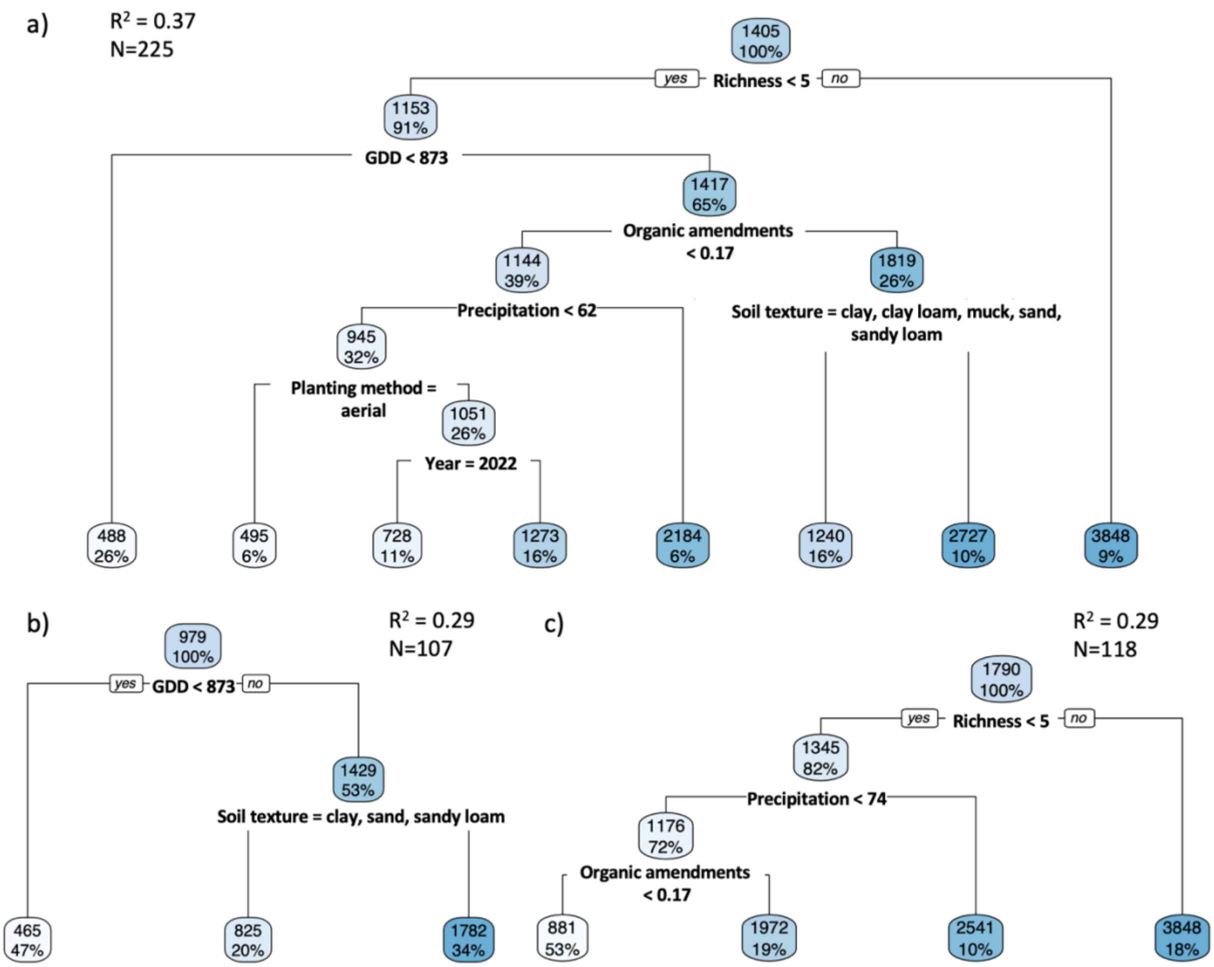

Figure 3-3: Regression trees predicting cover crop biomass for a) the full dataset (rye + mixtures), b) cereal rye, and c) mixtures. Ovals include mean biomass (kg ha^{-1}) and the percent of fields in each subgroup; darker shades of blue indicate higher mean biomass.

3.4 Discussion

3.4.1 Mixtures outperform cereal rye across farms

Our novel citizen science approach goes beyond quantifying cover crop performance on working farms, which was highly variable, to also identifying key factors driving performance. We hypothesized that mixtures and cereal rye would produce similar levels of biomass overall, in part because mixtures involve greater management complexity, but instead found that, on average, cover crop mixtures accumulated twice as much biomass and N as rye. This was likely driven by a critical distinction between management of rye and mixtures. Cereal rye is the most widely used cover crop in the region, in part because it can establish during the cold and short cover crop windows in simplified cropping systems commonplace in the Midwest (CTIC-SARE-ASTA, 2023). Yet, these simplified rotations also limit the potential for meaningful cover crop growth and associated benefits. Mixtures were more likely to be planted in diversified systems that included small grains, which offer warmer and longer post-harvest cover crop growing windows ideal for establishing diverse mixtures that can accumulate substantial biomass and N. This demonstrates a synergistic relationship between increasing primary crop and cover crop diversity, which can increase cover crop biomass inputs to soil, support greater internal nutrient cycling, and reduce the need for environmentally and economically costly inputs like synthetic fertilizers and pesticides (Blesh, 2018; Ruis et al., 2019).

3.4.2 Regression trees reveal leverage points for optimizing cover crop management

In accordance with our hypothesis, cereal rye and mixture performance were constrained by different factors because they tended to occupy distinct niches. Cereal rye biomass was driven by GDD, reflecting the value of identifying strategies for extending the rye growing season

(McClelland et al., 2021; Lawson et al., 2015). Farmers can achieve earlier rye planting dates by interseeding into standing corn or soybeans (Brooker et al., 2020; Moore and Mirsky, 2020), or delay termination in the spring by planting green (i.e., waiting to terminate cover crops until after cash crop planting). In fact, a recent national survey indicated that 61% of cover crop users now plant green (CTIC-SARE-ASTA, 2023) given experimental evidence that it can improve cover crop performance (Reed and Karsten, 2022). Despite strong potential for such practices to extend the cereal rye growing window, two-thirds of all rye fields in this study still failed to reach 1.0 Mg ha^{-1} of biomass. The low rye biomass and N assimilation estimates in our study indicate that nutrient retention was likely not occurring at levels sufficient for addressing water quality issues (Hively et al., 2009), and underscore a substantial need for improved management. Notably, a long rye growing season combined with loam, silt loam, or clay loam soil led to the greatest rye biomass, highlighting that biomass expectations should account for edaphic factors.

Many mixtures were planted earlier in the fall than cereal rye and their performance was therefore not constrained by GDD, but rather by precipitation, particularly for those with lower species richness. Farmers in the USA Great Lakes region are grappling with more variable precipitation patterns due to climate change, including periods of heavy rainfall coupled with drought in between (Wilson et al., 2023). That high diversity mixtures performed best suggests that increasing species richness may offer “insurance” across heterogenous environmental conditions, such as weather and soil textures, because it increases the chances of at least a few species doing well (Tilman, 1996; Mariotte et al., 2013; Yachi and Loreau, 1999). Higher diversity mixtures may also exhibit greater niche complementarity that enhances productivity (Blesh, 2018; Finney and Kaye, 2017; Cardinale et al., 2007), such as through differences in root traits that increase resource-use efficiency (Reiss and Drinkwater, 2018; Gross and Glaser, 2021). For the 82% of mixtures with fewer than five overwintering species, ecological management approaches helped mitigate the effects of low precipitation. Specifically, mean cover crop biomass in fields with more regular organic amendment applications was reduced by only 22% under low precipitation compared to 65% in fields with little to no use of organic amendments. Organic inputs, such as manure and compost, build soil organic matter, which improves water infiltration and retention and increases internal nutrient cycling capacity (Oldfield et al., 2018; Ruis et al., 2019). In turn, those fields may experience greater resilience to variable precipitation patterns.

The positive effect of organic amendments on biomass also appeared in the combined analysis for rye and mixtures, and highlights important feedbacks when multiple ecological practices were used together. Specifically, regular use of organic amendments may increase cover crop biomass and nutrient recycling. This also suggests that, over time, farmers could increase reliance on cover crops to maintain soil carbon and nutrient reserves, reducing the need for external inputs. Additionally, our results indicate that interactions between management history and environmental conditions affect outcomes of other cover crop management decisions, such as planting method. Infrequent organic amendment inputs combined with low precipitation resulted in poor growth for aerially-seeded cover crops. Given this, farmers in soils with lower organic matter levels may benefit from cover crop planting methods that maximize seed-soil contact (Zhao et al., 2022). Our findings that cover crop management should be tailored based on context echoes similar calls for precision management of compost and manure in other aspects of agriculture (Swoish et al., 2022). Relatedly, farmers might consider trade-offs in using cereal rye versus mixtures depending on their rotation and farming conditions given that both have potential to perform well. For instance, although mixtures outperformed cereal rye overall in this study, rye may be the only suitable option following late fall corn harvest, but can still accumulate substantial biomass and N if allowed to grow well into spring, especially in loamy soils.

3.4.3 Citizen science as a collaborative cover crop research and monitoring tool

The citizen science approach presented here can improve current efforts to increase cover crop adoption across the globe by identifying successful cover crop management strategies across different farming conditions. Because farmers often cite the experiences of other farmers as one of their most trusted resources (Asprooth et al., 2023), our approach leveraging data from real farms produces actionable and practical management recommendations. Expanded implementation to build a larger dataset would enable greater explanatory power and development of more nuanced regression trees. For instance, to provide farmers with more context-specific and management-relevant information, data could be analyzed by different subgroups, such as by soil type, preceding crop, or state. Additional data on cover crop mixture performance and composition would enable identifying whether the benefits of increasing species richness taper off at a certain level. Importantly, the voluntary nature of our study means the management practices and cover crop outcomes captured here may not be fully reflective of the general farming population. Our study participants were likely more inclined towards on-farm experimentation and sustainable management than most farmers, such that future research would benefit from targeted efforts to include a broader suite of participants to ensure results are applicable to different types of farmers.

That cover crop performance was highly variable across fields in our study underscores that, despite their potential for addressing environmental crises, suboptimal implementation of conservation practices is constraining their impact under real world conditions. Cover crop incentive programs aimed at sequestering carbon, building soil health, and reducing nutrient pollution would benefit from expanding beyond participation-based program structures to those that also consider performance (Asprooth et al., 2023). Our field assessment protocol could be easily deployed to track cover crop biomass on enrolled fields and identify areas for targeted technical assistance to improve cover crop performance. The citizen science framework used here could also inform management guidelines that are linked to improved outcomes, such as threshold levels of diversity or growing degree days.

3.5 Conclusion

Using a novel citizen science approach, we compiled a unique cover crop dataset with both breadth and depth to evaluate if and how farmers are successfully using cover crops in the Great Lakes region. We found that cover crop mixtures accumulated roughly twice as much biomass and nitrogen, on average, compared to cereal rye, in part because they were planted as part of more diverse rotations. This offers compelling evidence for farmers considering diversifying their rotations with small grains that the synergistic benefits with cover crops are substantial. Using high diversity cover crop mixtures in particular helped ensure successful cover crop growth across different farming conditions, while benefits from rye were constrained by short growing seasons. That nearly one-third of regional variation in cereal rye and mixture biomass was explained by just two and three variables, respectively, highlights the utility of our approach for identifying the most crucial leverage points for adapting management. In sum, the citizen science approach presented here contributes valuable information on key opportunities for improving sustainability outcomes of cover crops and paves a path forward for continued researcher-practitioner collaboration.

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3.7 Supplemental Material

Table 3-4: Farm and field sample sizes by year and state. Participants were invited to enroll any cover crop type on their farm, though in this analysis we focused on cereal rye and mixtures, which comprised the majority of enrolled fields. Other cover crop types included winter wheat, crimson clover, red clover, and triticale (N=27, or 10.7% of all fields).

	State	**MI**	**OH**	**IN**	**IL**	**WI**	**MN**	***Total***
2022	Farms	20	5	5	2	23	2	57
	Fields	61	10	7	5	34	8	125
	Mixture	32	5	6	2	13	6	64
	Cereal rye	21	5	1	3	18	0	48
2023	Farms	14	15	10	12	13	6	70
	Fields	24	29	19	24	21	11	128
	Mixture	10	10	8	14	9	3	54
	Cereal rye	12	15	11	10	7	5	60
Total	Farms	27	16	13	13	26	7	102
	Fields	85	39	26	29	55	19	253
	Mixture	42	15	14	16	22	9	118
	Cereal rye	33	20	12	13	25	5	108

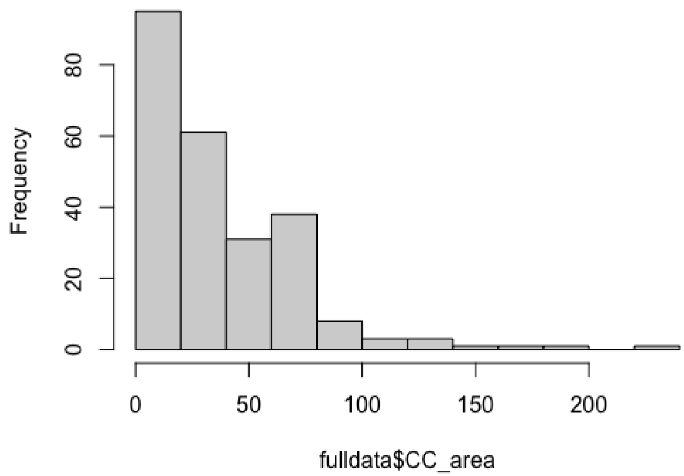

Figure 3-4: Distribution of cover crop field sizes (ha) in the study.

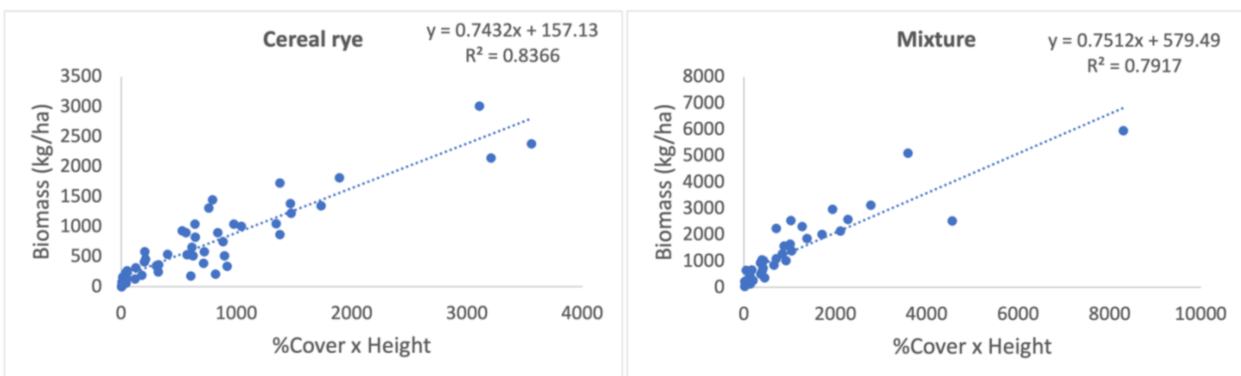

Figure 3-5: Biomass validation relationships for the field assessment protocol for cereal rye (left; N = 55) and mixture cover crop fields (right; N = 38).

Table 3-5: Summary statistics for nitrogen concentration (%N) of biomass validation samples collected from a subset of participating fields.

Species		**%N**		
	Sample size	*Min*	*Max*	*Mean*
Legumes				
Balansa clover (*Trifolium michelianum*)	4	3.08	3.40	3.16
Berseem clover (*Trifolium alexandrinum*)	1	n/a	n/a	2.63
Crimson clover (*Trifolium incarnatum*)	38	1.87	4.44	2.86
Red clover (*Trifolium pratense*)	6	3.16	3.83	3.45
Sweet clover (*Melilotus officinalis*)	5	3.44	4.31	3.82
Clover+ (*Trifolium*)	3	2.49	3.58	3.07
Austrian winter peas (*Pisum sativum*)	8	2.48	5.69	3.77
Common vetch (*Vicia sativa*)	1	n/a	n/a	4.08
Hairy vetch (*Vicia villosa*)	15	2.06	4.43	3.54
Vetch+ (*Vicia*)	6	3.70	4.18	4.01
Grasses				
Annual ryegrass (*Lolium multiflorum*)	2	2.07	3.40	2.74
Barley (*Hordeum vulgare*)	6	1.10	2.97	2.01
Cereal rye (*Secale cereale*)	86	1.12	4.91	2.81
Oats (*Avena sativa*)	1	n/a	n/a	3.45
Triticale (*Secale cereale x Triticum aestivum*)	2	0.92	1.97	1.45
Winter wheat (*Triticum aestivum*)	5	2.38	3.18	2.84
Brassicas				
Dwarf-essex rapeseed (*Brassica napus*)	19	1.81	5.82	2.99
Flax (*Linum usitatissimum*)	2	2.14	2.73	2.44
Kale (*Brassica oleracea*)	3	1.74	1.86	1.80
Turnip (*Brassica rapa*)	3	3.74	5.37	4.47
Other				
Chicory (*Cichorium intybus*)	4	1.87	4.21	3.56
Weeds	79	1.23	4.65	2.47

+Species/Variety not stated

Chapter 4 – Increasing Crop Rotation Diversity with Cover Crops Builds Climate Resilience on Working Farms[3]

Abstract

Farms in the U.S. Great Lakes region are experiencing disruptive heavy rainfall during the spring planting window and more intense droughts during the summer growing season. We used field-scale remote sensing to assess relationships between crop diversification and agroecosystem climate resilience in Michigan, an important and diverse agricultural state in the Great Lakes, from 2008 to 2019. Recent analyses of field experiments suggest that increasing crop rotation complexity builds resilience to climate change, especially when rotations include overwintering cover crops (i.e., non-harvested crops) because they maintain continuous living cover, retain nutrients, and increase organic matter inputs to soil. However, evidence from working farms is lacking. Using panel fixed effects models and linear regressions, we assessed how corn and soybean yield and temporal yield stability (measured as the coefficient of variation) respond 1) to an index of crop rotation complexity that encompasses species turnover and diversity, and 2) more specifically to replacing bare fallows with winter cover crops. We also tested how cover crops influence corn and soybean planting dates as an indicator of resilience to heavy spring rainfall. Corn and soybean yields increased with rotation complexity ($p<0.001$), especially for soybean, but yield stability for both crops decreased with increasing rotation complexity ($p<0.001$). In fields with at least three years of cover crops during the 12-year study period,

[3] Chapter 4 is prepared for submission to Global Change Biology with co-authors Meha Jain, Kent Connell, Haoyu Wang, Weiqi Zhou, and Jennifer Blesh.

cover crop use had a positive effect on corn and soybean yields ($p<0.001$), and on soybean yield stability ($p=0.04$), but no significant effect on corn yield stability. Furthermore, spring planting delays under heavy rainfall were reduced as prior years of cover crops increased ($p<0.001$). Our findings suggest that diversifying crop rotations, particularly with winter cover crops, has strong promise for increasing agroecosystem climate resilience.

4.1 Introduction

Increasingly variable and extreme precipitation patterns due to global climate change, including more frequent floods and droughts, pose major challenges for agricultural production (Trenberth, 2011). In response, a growing body of literature now explores strategies for improving agroecosystem resilience to climate change, including through crop rotation diversification, or increasing the number and types of species grown through time. In addition to providing numerous regulating and supporting ecosystem services (Beillouin et al., 2021; Tamburini et al., 2020), increasing crop diversity on farms has potential to maintain yields and build resilience to climate shocks (Birthal & Hazrana, 2019; Bowles et al., 2020; Degani et al., 2019; Gaudin, Tolhurst, et al., 2015a; Lotter et al., 2003; Marini et al., 2020; Renwick et al., 2021). This may be especially true when adding crops that have different functional traits and roles in the ecosystem (Smith et al. 2023; Costa et al. 2024).

Functionally diverse rotations can have improved resource-use efficiency and soil quality that help mitigate the negative effects of variable and extreme climatic conditions (Isbell et al., 2017; Tanaka et al., 2005; Wang et al., 2018). In the U.S. Midwest, agriculture is dominated by simplified grain rotations with winter bare fallows in between. Replacing these bare fallows with species that fill the overwintering niche is an outstanding opportunity for increasing crop functional diversity. Species that overwinter help maintain continuous living cover, reduce erosion, and minimize nutrient losses (Tonitto et al., 2006). Common options include small grains like winter wheat, or perennial forages like alfalfa. Increasingly, farmers are also using overwintering cover crops to enhance agroecosystem diversity and function, with a four-fold increase in cover crop adoption in the U.S. Midwest from 1.8% to 7.2% over the past decade (Zhou et al., 2022). Meta-analyses have shown that diversifying rotations with non-harvested winter cover crops has strong potential to build soil organic matter (SOM) (King & Blesh, 2018; McDaniel et al., 2014); SOM then supports functions critical to resilient agroecosystems, including nutrient cycling, soil structure, water infiltration and retention, and productivity (Hudson, 1994; Kane et al., 2021; Williams et al., 2016).

Despite these benefits, evidence of cover crop effects on primary crop yield and yield stability is mixed (Basche et al., 2016; Hunter et al., 2019; Li et al., 2019; Marcillo & Miguez, 2017; Nouri et al., 2020). This is in part because yield responses to cover crops may be driven by a combination of legacy and immediate effects. Although improved soil quality from long-term cover crop use (i.e., legacy effects) could buffer against variable weather patterns to create more stable yields through time (Nouri et al., 2020; Renwick et al., 2021; Williams et al., 2016), cover crops grown immediately preceding a cash crop can also reduce yields by depleting soil water and nutrient availability (Hunter et al., 2021; Li et al., 2019; Martinez-Feria et al., 2016). Yield reductions are also a concern when cover crops delay primary crop planting (Myers & Wilson, 2023; R. Myers & Watts, 2015; Surdoval et al., 2024). However, under climate change, cover crops may instead reduce risk of planting delays under heavy spring rainfall, which is an increasingly common precipitation pattern in the Midwest (CTIC-SARE-ASTA, 2020; Sherrick & Meyers, 2023). In this case, cover crops may have positive legacy and immediate effects: long-term use improves water infiltration and retention (Haruna et al., 2020), and cover crops grown immediately prior to cash crop planting can increase transpiration, though greater ground cover from cover crops could offset this positive effect if it reduces soil surface evaporation.

Most evidence for the benefits of increasing crop diversity comes from research station experiments with relatively controlled conditions that may not fully reflect outcomes on working farms. For instance, they are often conducted at smaller spatial scales that miss field- and farm-scale dynamics (Kravchenko et al., 2017; Stanley et al., 2024). It is also difficult to replicate farmer decision making in these contexts because producers adapt their management to a complex set of environmental, political, social, and economic factors (Epanchin-Niell et al., 2022). Remote sensing offers a promising approach for assessing crop diversification on farms at large spatiotemporal scales. A recent remote sensing analysis corroborated results of field experiments showing that cover crops are associated with small corn and soybean yield declines (Deines et al. 2023), but did not parse out immediate versus legacy effects. Another remote sensing study suggested cover crops have negative to neutral effects on corn and soybean yields in drought years, but did not assess temporal yield stability (Kc & Khanal, 2023). To our knowledge, only one study has used remote sensing to quantify crop rotation complexity on farms (Socolar et al. 2021), and none have linked rotation complexity to agroecosystem climate resilience. It thus remains unclear whether crop diversification on working farms translates into greater climate resilience.

We address this knowledge gap by using remote sensing to assess relationships between crop diversification and corn and soybean yield and temporal yield stability in Michigan from 2008-2019. To quantify field-scale rotation diversity we developed an index of overall crop rotation complexity that integrates crop sequence (i.e., turnover) and the number and types of crops in rotation. We also separately evaluate the use of non-harvested winter cover crops. We parse out the effects of past cover crop use (i.e., legacy effects) versus current cover crop status (i.e., immediate effects) given that they may have divergent effects driven by different mechanisms. Moreover, because it can take at least three years of cover cropping for appreciable soil improvements to occur (Blesh, 2019; Cates et al., 2019; Nyabami et al., 2024; Wood & Bowman, 2021), we examine how winter cover crop effects on yield and yield stability differ depending on years of use. Finally, we also test how winter cover crops influence corn and soybean planting dates as an indicator of resilience to heavy spring rainfall.

We hypothesize that corn and soybean yield and yield stability will increase with crop rotation complexity, but winter cover crops will have divergent immediate and legacy effects. Specifically, having an overwintering cover crop growing in the spring immediately prior to cash crop planting (i.e., current cover crop status) will reduce yield. Conversely, we expect that cover crop legacy will be associated with increased yields and yield stability, particularly after at least three years of cover crop use due to soil improvements. We also hypothesize that planting delays will be smaller in fields with cover crops growing in the spring, and a longer history of cover crop use will strengthen this effect. This study using novel remote sensing approaches is, to our knowledge, the most comprehensive and robust test of relationships between crop diversification and climate resilience on working farms in the U.S. Midwest to date.

4.2 Methods

4.2.1 Study area

We analyzed relationships between crop diversification and agroecosystem climate resilience in the lower peninsula of Michigan in the U.S. Midwest, where climate change is bringing increasingly heavy spring rainfall and more frequent and severe droughts during the summer growing season (Wilson et al., 2023). As the second most agriculturally diverse state in the country, Michigan is well-suited for this study because it contains not only conventional corn-soybean rotations, but also more diverse systems with small grains, alfalfa, and numerous other crop species (MDARD, 2023). It also contains hotspots of cover crop adoption (Seifert et al., 2018; Surdoval et al., 2024), in part driven by efforts to protect surrounding freshwater resources from nutrient pollution (Michalak et al., 2013). Further, a wide range of soil types and climatic conditions across the state allows for representation of diverse environmental conditions in our analyses.

4.2.2 Data and sources

Our dataset, compiled at the field scale from 2008-2019, included the USDA NASS Cropland Data Layer (CDL), corn and soybean planting dates and yields, field size, National Commodity Crop Productivity Index (NCCPI) from gSSURGO (Dobos et al. 2012), precipitation and growing degree days (GDD) derived from PRISM Climate Group, a crop rotation complexity index, current cover crop status in a given year, and years of prior cover crop use.

4.2.2.1 Crop data

We used the USDA NASS Cropland Data Layer (CDL) to extract data on the crops grown in each field from 2008 to 2019. Corn and soybeans are mapped with high accuracy in the CDL and comprise roughly half of Michigan's agricultural land area (USDA NASS, 2019), so our planting date (day of year) and yield (Mg ha^{-1}) variables focus on these two crops.

To derive the planting date and yield data, we combined Normalized Difference Vegetation Index (NDVI) data from 250 m resolution, 16 day MOD13 Q1.006 Terra and MYD13 Q1.006 Aqua datasets in Google Earth Engine to create an 8 day NDVI data product (Gorelick et al., 2017). We used the QA data layer to keep good quality pixels and remove the effects of snow, ice, and cloud cover. Because January and February images had >80% missing pixels due to snow and cloud cover, we excluded those images, for a total of 38 images per year. For each year from 2008-2019, we then selected all pixels that planted corn and soybean based on the CDL, and resampled the CDL data to match the MODIS resolution of 250m. Next, we used TIMESAT version 3.3 (Eklundh & Jönsson, 2017) to extract the start, middle, and end of season dates, and area under the curve. We used default TIMESAT parameters, except for using the double logistic fitting model; setting the 'No. of season' to one growing season per year; and setting the 'Seasonal amplitude' for 'season start' and 'season end' to 0.3 instead of 0.5 (Urban et al., 2018). We did not have ground data to validate our planting date estimates, however, TIMESAT start of season parameters have been well validated elsewhere (Rodigheri et al., 2023).

We present distributions of start of season across all pixels in our study region as well as mean planting date in Figure S4-6. To validate the yield data, we used the USDA NASS Quick Stats annual county-level yield and planted area data for corn and soybean from 2008 to 2019. Specifically, we multiplied the county-level yield by planted area, and compared those data to the sum of the area under the curve from TIMESAT (Figures S4-7 and S4-8). Area under the curve was then translated to actual yield by regressing county-level yield as reported in the census data on area under the curve as estimated using TIMESAT. These regression coefficients were then applied to the area under the curve estimates to translate them to yield (Mg ha^{-1}).

The cover crop variable is based on a map produced using Landsat satellite and CDL data, where we separated winter cover into five classes: bare, low biomass (i.e., weedy fallows), winter wheat, alfalfa hay, and overwintering cover crops. The winter wheat and alfalfa hay classes are based on data reported in the CDL, where they are mapped with high accuracy, while full methods for development of the cover crop class, including field data collection, algorithm development, and model accuracy, are detailed in Surdoval et al. (2024).

4.2.2.2 Environmental data

To control for differences across fields in land productivity potential, we used the NCCPI from gSSURGO (Dobos et al. 2012). Daily precipitation and temperature data were extracted from PRISM Climate Group. For each field, we summed precipitation across April and May to calculate total spring precipitation. For total precipitation during the primary crop growing season, we summed daily precipitation across June, July, and August, when water demand from corn and soybean is greatest. We also calculated GDD during the corn and soybean growing season from May through August, with a base temperature of 10°C, as:

$$GDD = Average\ Daily\ Temperature\ (°C) - Plant\ Baseline\ Growing\ Temperature\ (°C)$$

4.2.2.3 Crop diversification metrics

For each field in the dataset, we calculated years of overwintering cover crops (CC years) and overall rotation complexity (RC). In each year, CC years was calculated as the total number of times an overwintering cover crop had appeared in the field since 2008. Our rotation complexity index combined the cover crop variable with all other crop species reported in the CDL to account for species richness and turnover and the diversity of crop functional groups in rotation. It modifies and extends the index presented in Socolar et al. (2021) by giving greater weight to crops and practices with known ecological benefits, specifically perennials, intercrops, and overwintering cover crops (King & Blesh, 2018). For each 6-year crop sequence (i.e., from 2008-2013, 2009-2014, etc.) in a field, we calculated rotation complexity as:

$$RC = \sqrt{\left(\frac{T_1+T_2+T_P+T_I}{2}\right) + T_C} * N$$

where T_1 is the number of times a crop was grown that was not grown the year before; T_2 is the number of times a crop was grown that was not grown two years before; T_P is the number of years a perennial crop was grown; T_I is the number of years an intercrop was grown (as indicated in the CDL); T_C is the number of a times a cover crop was used; and N is the number of unique species in the rotation. Using this index, a continuous corn rotation would receive a score of 0; a corn-soy rotation with no cover crop would receive a score of 3.16; four years of alfalfa followed by corn-soy would receive a score of 6; and a corn-soy-wheat rotation with cover crops would receive a score of 7.65.

4.2.3 Statistical analysis

To test for relationships between crop diversification and corn and soybean yields, we used the plm package in R version 4.2.1 to run panel fixed effects regression models, which help address issues of omitted variable bias:

$$yield_{it} = \beta_1 CD_{it} + \beta_2 CC_{it} + \beta_3 precip_{it} + \beta_4 GDD_{it} + \beta_5 plantdate_{it} + t + \varphi_i + \varepsilon_{it}$$

where $yield_{it}$ is corn or soybean yield in field *i* at year *t*, $\beta_1 CD_{it}$ denotes the crop diversification metric – CC years or RC – in field *i* at year *t*, $\beta_2 CC_{it}$ denotes "immediate" cover crop status as a factor (i.e., if a cover crop is present or not) in field *i* at year *t*, $\beta_3 precip_{it}$ is total precipitation (mm) during the primary crop growing season in field *i* at year *t*, $\beta_4 GDD_{it}$ is total GDD during the primary crop growing season in field *i* at year *t*, $\beta_5 plantdate_{it}$ is corn or soybean planting date in field *i* at year *t*, *t* is year, φ_i is a field fixed effect, and ε_{it} is the error term. Because it may take several years of cover crop use for soil and yield improvements to occur, and because our dataset is skewed towards fields with short-term cover crop use (Figure 4-1), we ran separate panel fixed effects regressions for fields with less than three (< 3) years of cover crop use and those with three or more (3+) years of cover crop use. Yields were log transformed to meet assumptions of normality and homoskedasticity and to allow for estimating the percent change in yield in response to the diversification practices included in the models.

To evaluate whether crop diversification was associated with greater yield stability, we used the coefficient of variation (CV) of corn and soybean yields in each field as an indicator of temporal yield stability. For each crop, we first selected fields with at least three years of yield data for corn or soybean. From that subset of fields, we then randomly sampled three years of yield data for either corn or soy from each field to calculate the CV. Because the resulting datasets were cross-sectional, we used multiple linear regressions, rather than panel regressions, as follows:

$$cv_i = \beta_1 CD_i + \beta_2 NCCPI_i + \beta_3 meanyield_i + \beta_4 fieldsize_i + county_i + \varepsilon_i$$

where cv_i indicates the CV for corn or soybean yield in field i, $\beta_1 CD_i$ is the crop diversification metric – total CC years or average RC – in field i, $\beta_2 NCCPI_i$ is NCCPI for field i, $\beta_3 meanyield_i$ is the mean yield (Mg ha^{-1}) for corn or soybeans in field *i* from 2008 to 2019, $\beta_4 fieldsize_i$ is the size of field *i* (ha), $county_i$ denotes the county in which field *i* is located as a fixed effect, and ε_i is the error term. We included mean yield and field size to control for the tendency for farmers to use diversification practices on the lowest yielding and most marginal fields (Blesh & Drinkwater, 2013; Seifert et al., 2018; Sherrick & Meyers, 2023; Socolar et al., 2021), which would otherwise bias results. We also included county as a fixed effect to help control for spatial autocorrelation. Similar to the yield models, we ran separate models for fields with < 3 versus 3+ years of cover crop use. All continuous explanatory variables were scaled and centered to a mean of 0 in the yield stability models, and CV was square root transformed to meet assumptions of normality and homoskedasticity.

To assess the effects of cover crop use on corn and soybean planting dates, we used panel fixed effects regression models:

$$plantdate_{it} = \beta_1 CCyrs_{it} + \beta_2 CC_{it} + \beta_3 precip_{it} + \beta_{123}(CC_{it} \times CCyrs_{it} \times precip_{it}) + t + \varphi_i + \varepsilon_{it}$$

where $plantdate_{it}$ indicates corn or soybean planting date in field *i* at year *t*, $\beta_1 CCyrs_{it}$ is years of cover crop use in field *i* at year *t* since 2008, $\beta_2 CC_{it}$ denotes cover crop status as a factor in field *i* at year *t*, $\beta_3 precip_{it}$ is total spring precipitation (mm) in field *i* at year *t*, $\beta_{123}(CC_{it} \times CCyrs_{it} \times precip_{it})$ is a three-way interaction between cover crop status, years of cover crop use, and spring precipitation, *t* is year, φ_i is a field fixed effect, and ε_{it} is the error term.

4.3 Results

4.3.1 Patterns of crop diversification

Across all fields, the distribution of CC years was positively skewed, while RC was more symmetrically distributed (Figure 4-1). Means and standard deviations differed between the yield and yield stability datasets, though (Table S4-4). In general, the yield datasets had slightly higher mean values for the diversification metrics than the yield stability datasets, reflecting that the yield stability datasets only include fields with at least three years of corn or soybean. Both CC years and RC showed relatively large variation (Table S4-4). We also found distinct trends between crop diversification and several field attributes: CC years and RC decreased with increasing mean yield, NCCPI, and field size, though the effect was less pronounced for RC than for CC years (Table S4-5).

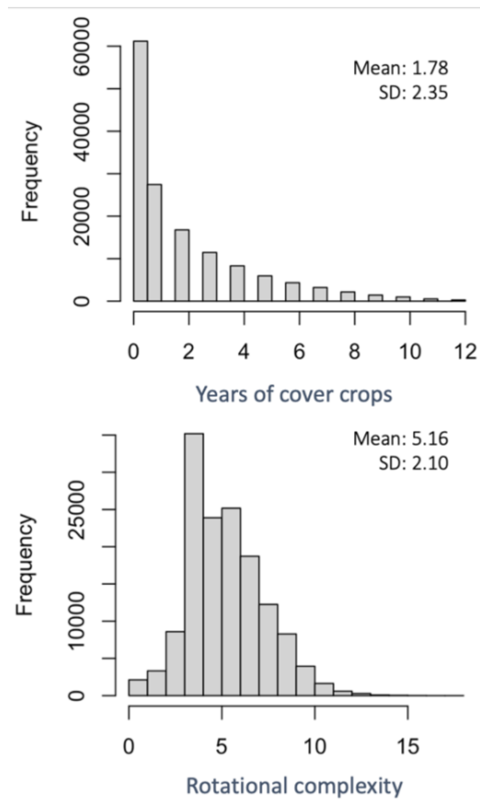

Figure 4-1: Distribution of fields across the full dataset for years of cover crop use (top) and the rotation complexity index (bottom), with means and standard deviations (SD). N = 144138.

Aside from the bare and low biomass (i.e., weedy) winter cover classes, cover crops were the most frequently occurring form of winter cover across the datasets (Figure 4-2). Based on the CDL, farmers in Michigan integrated a range of primary crops beyond corn and soybean into rotation, including winter wheat, alfalfa, pasture, dry beans, and sugarbeets (Figure 4-3). The corn datasets had a higher percentage of alfalfa, and slightly lower percentage of winter wheat observations, compared to the soybean datasets. Notably, compared to the yield datasets, corn and soybean together comprised a higher percentage of primary crop observations in the yield stability datasets, reflecting potential bias towards less diverse fields for those datasets.

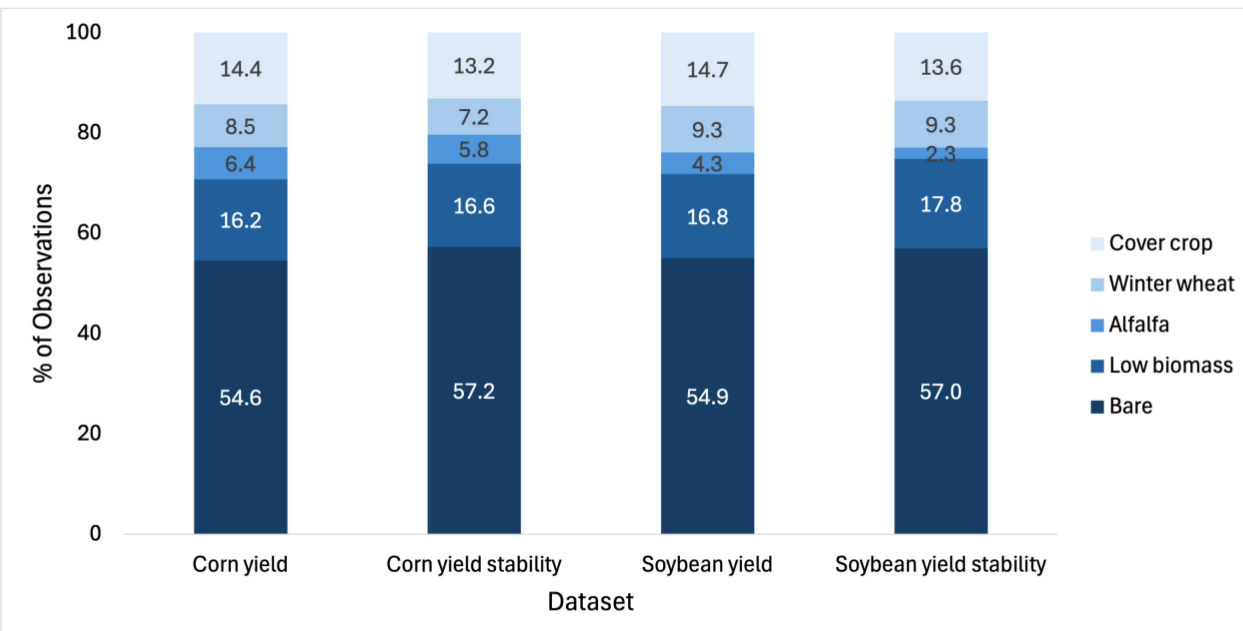

Figure 4-2: Winter cover in Michigan. For each dataset, the percentage of observations classified as cover crop, winter wheat, alfalfa, low biomass, or bare are shown according to the color-coded legend based on the winter cover variable described in Section 4.2.2.1.

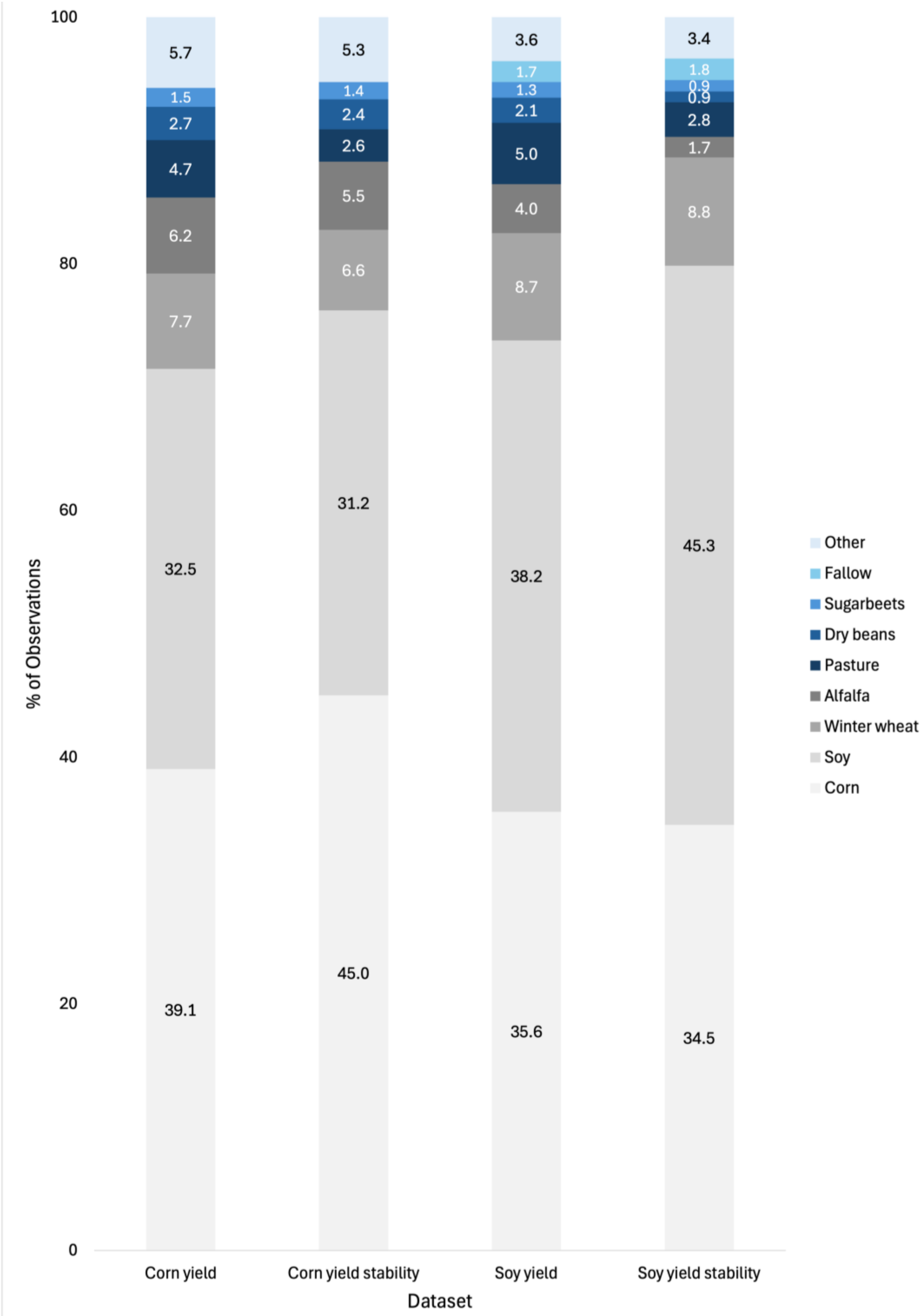

Figure 4-3: Percentage of observations for different crop categories (corresponding to colored legend) in each dataset based on data reported in the CDL. Crop categories comprising < 2% are grouped together in "Other."

4.3.2 Crop diversification effects on yield and yield stability

Corn yield increased by 0.2% ($p<0.001$), and soybean yield by 0.6% ($p<0.001$), for every one-unit increase in rotation complexity (Figure 4-4). For context, two cycles of a corn-soy- wheat rotation with cover crops (RC=7.65) corresponded to 1.53% higher corn yield compared to a continuous corn rotation (RC=0), and 4.59% higher soybean yield compared to a continuous soybean rotation (RC=0). When considering corn fields with < 3 CC years, each year of cover crop use was associated with a 1.3% increase in corn yield, and this effect increased to 1.5% per year of cover crop use for fields with 3+ CC years ($p<0.001$; Figure 4-4). For soybean fields with < 3 CC years, regression results indicated no significant change in soybean yields with years of

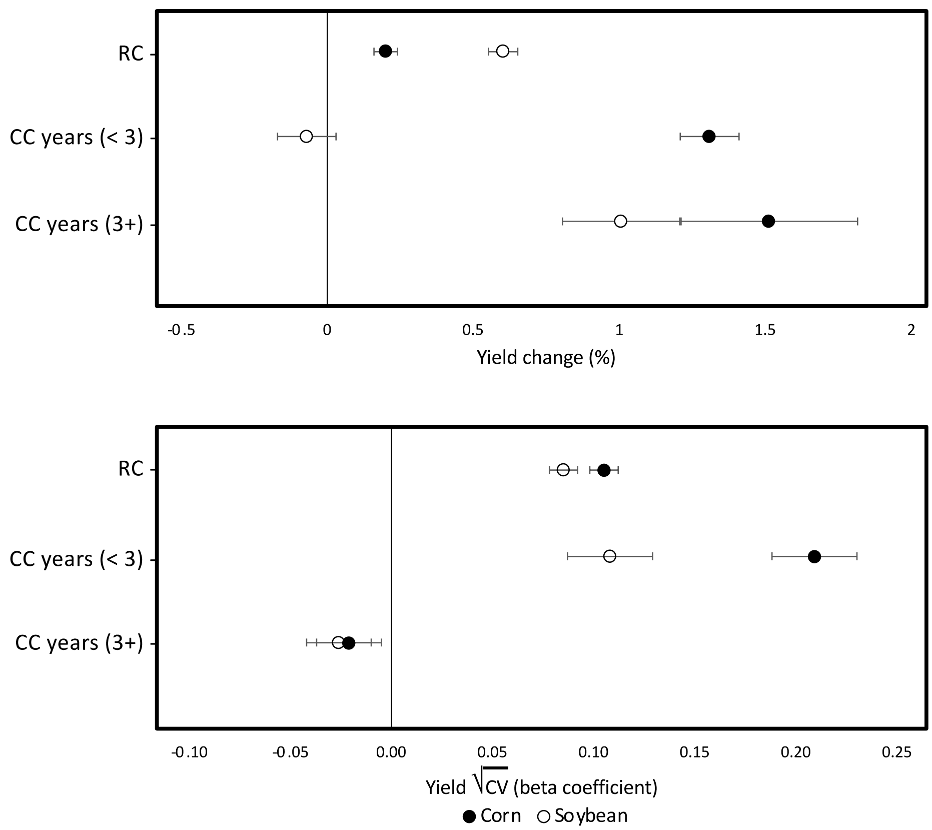

Figure 4-4: Top: Percentage change in corn and soybean yield for a one-unit increase in rotation complexity (RC) or years of cover crops (CC years) based on regression models. Bottom: Yield stability beta coefficients, specifically for square-root transformed corn and soybean CV in response to RC and CC years. Models for CC years are shown for fields with less than three (< 3) years of cover crops, and those with at least three years (3+) of cover crops.

cover crops, but this changed to a 1.0% increase for each year of cover crop use when analyzing fields with 3+ CC years ($p<0.001$; Figure 4-4). In contrast to the legacy effects, immediate cover crop effects on yields were negative (i.e., winter cover crops grown immediately prior to cash crop production reduced corn and soybean yields) ($p<0.001$) (Table 4-1). Yield stability models showed positive relationships between crop diversification and corn and soybean CV, indicating lower yield stability with greater diversity, except for fields with 3+ CC years (Figure 4-4; Table 4-2). In fields with 3+ CC years, years of cover crop use was negatively related to soybean CV at ecologically relevant levels (i.e., greater yield stability; $p=0.10$), and had no significant effect on corn yield stability.

4.3.3 Effect of cover crops on corn and soybean planting dates

Holding all other variables constant at their mean, having a cover crop growing in the spring immediately prior to cash crop planting delayed the corn planting date by 2.68 (±0.38) days ($p<0.001$), on average, but had no significant effect on soybean planting date (Table 4-3). Furthermore, there was a positive relationship between CC years and planting date for both corn and soybean, suggesting that farmers with more cover crop experience plant their cash crops later in the spring ($p<0.001$). We also found significant interactions between CC years and spring precipitation (Table 4-3; Figure 4-5). As precipitation increased above average (~240mm), fields with no history of cover crop use experienced substantial planting delays; however, these planting delays decreased with each year of prior cover crop use. This effect was stronger for corn ($p<0.001$) than for soybean ($p<0.01$). Additionally, as spring rainfall increased, the immediate effect of a current cover crop on planting date was moderated by past cover crop use ($p<0.001$). If the field contained a cover crop for the first time, the planting delay under above

Table 4-1: Regression coefficients for panel fixed effects models testing the effects of rotation complexity (RC) and years of cover crop use (CC years) on log-transformed corn and soybean yields. “CC status” is the effect of having an overwintering cover crop pr present in the spring immediately prior to cash crop production. Models for CC years are shown for fields with < 3 years of cover crops, and those with 3+ years of cover crops. DoY = Day of Year.

Corn yield model	*RC*	*CC years*	*CC status*	*Precipitation (mm)*	*GDD (C)*	*Planting date (DoY)*	*Year*	*n (unique fields)*	*N (total observations)*	*R^2*	*F statistic*
Rotation complexity	0.002*** (0.0004)		-0.103*** (0.002)	0.0003*** (0.000008)	-0.0006*** (0.000006)	0.004*** (0.00004)	-0.022*** (0.0003)	113899	299862	0.18	6559 df = 6; 185957
Cover crops (< 3 years)		0.013*** (0.001)	-0.106*** (0.001)	0.0005*** (0.000005)	-0.0005*** (0.000003)	0.002*** (0.00003)	0.004*** (0.0001)	117504	475566	0.13	8691 df = 6; 358056
Cover crops (3+ years)		0.015*** (0.002)	-0.098*** (0.003)	0.0007*** (0.00002)	-0.0009*** (0.00002)	0.0009*** (0.00009)	-0.011*** (0.001)	23067	52761	0.15	896 df = 6; 29688
Soy yield model											
Rotation complexity	0.006*** (0.0005)		-0.090*** (0.002)	0.0005*** (0.000009)	0.0004*** (0.000006)	0.001*** (0.00004)	-0.022*** (0.0003)	106510	285598	0.08	2748 df = 6; 179082
Cover crops (< 3 years)		-0.0007 (0.001)	-0.082*** (0.002)	0.0006*** (0.000006)	0.0002*** (0.000003)	-0.0007*** (0.00003)	0.01*** (0.0001)	105682	421147	0.07	4023 df = 6; 315459
Cover crops (3+ years)		0.010*** (0.002)	-0.086*** (0.004)	0.0008*** (0.00003)	0.0001*** (0.00002)	-0.0003*** (0.00009)	-0.011*** (0.001)	22476	50046	0.06	266 df = 6; 27564

Note: *p<0.05; **p<0.01; ***p<0.001

Table 4-2: Regression coefficients for models testing relationships between rotation complexity (RC) and years of cover crop use (CC years) on corn and soybean yield stability, where the response variable is the square root-transformed coefficient of variation fo for corn and soybean yields. Models for CC years are shown for fields with < 3 years of cover crops, and those with 3+ years of cover crops. NCCPI = National Commodity Crop Productivity Index.

Corn yield stability models	*Intercept*	*RCI*	*CC years*	*NCCPI*	*Mean yield (Mg ha⁻¹)*	*Field size (ha)*	*N*	*R^2*	*F statistic*
RCI	*5.93**** (0.219)	0.105*** (0.007)		-0.003 (0.007)	-0.602*** (0.007)	-0.054*** (0.007)	92017	0.12	191 df = 64; 91951
Cover crops (< 3 years)	*6.10**** *(0.230)*		0.209*** (0.021)	-0.009 (0.008)	-0.535*** (0.009)	-0.076*** (0.007)	73753	0.09	121 df = 63; 73688
Cover crops (3+ years)	*5.82**** *(0.686)*		-0.021 (0.016)	0.031* (0.015)	-0.757*** (0.017)	-0.004 (0.016)	18264	0.14	46 df = 62; 18201
Soy yield stability models									
RCI	*5.58**** (0.388)	0.085*** (0.007)		-0.006 (0.007)	-0.657*** (0.007)	-0.072*** (0.007)	81872	0.14	225 df = 57; 81814
Cover crops (< 3 years)	*5.75**** *(0.398)*		0.108*** (0.021)	-0.003 (0.008)	-0.621*** (0.008)	-0.089*** (0.007)	65116	0.12	154 df = 56; 65059
Cover crops (3+ years)	*5.70**** *(1.37)*		-0.026+ (0.016)	-0.021 (0.015)	-0.767*** (0.015)	-0.044** (0.016)	16756	0.15	55 df = 53; 16702

Note: +p<0.10; *p<0.05; **p<0.01; ***p<0.001

average rainfall was larger than if the field was left bare that spring. However, this effect was attenuated with each year of past cover crop use. Specifically, after 6 years the effects of both current and past cover crop use on the resilience of planting date to heavy spring rainfall became positive (Figure 4-5).

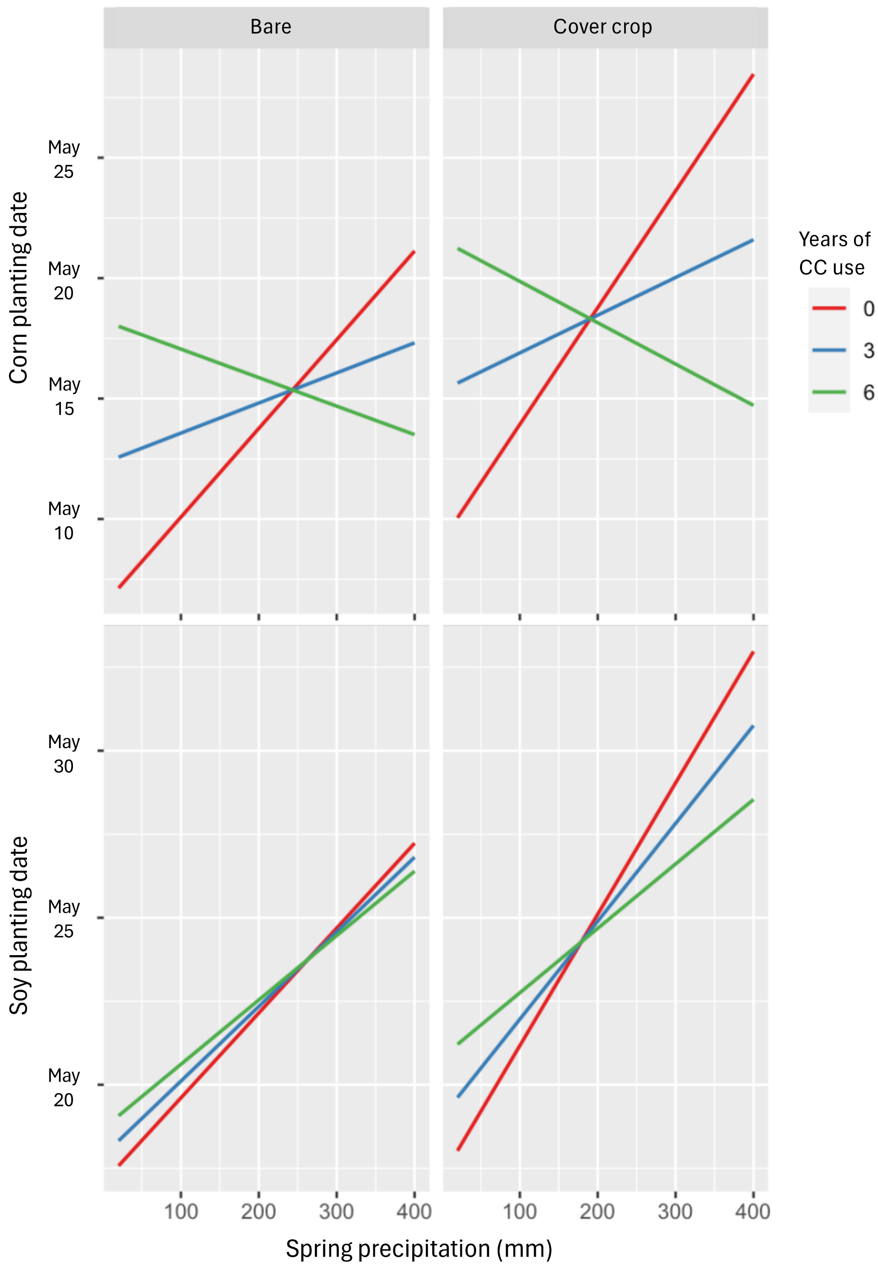

Figure 4-5: Interactions between spring precipitation, past cover crop use ("Years of CC use"), and current cover crop status ("Bare" versus "Cover crop") and their effects on corn and soybean planting dates.

Table 4-3: Regression coefficients for panel fixed effects regressions testing the effects of cover crops, spring precipitation (precip), and their interaction on corn and soybean planting dates. "CC" is the effect of having an overwintering cover crop present in the spring immediately prior to cash crop planting, whereas "CC years" is the number of years of prior cover crop use.

	Dependent variable:	
	Corn planting date	Soybean planting date
CC	2.68***	0.34
	(0.38)	(0.49)
CC years	1.97***	0.54***
	(0.13)	(0.15)
Spring precip (mm)	0.04***	0.05***
	(0.0004)	(0.001)
Year	1.63***	0.92***
	(0.01)	(0.01)
CC*Spring precip	0.01***	0.03***
	(0.002)	(0.002)
CC*CCyrs	0.11	0.66**
	(0.18)	(0.21)
CCyrs*Spring precip	-0.01***	-0.002**
	(0.001)	(0.001)
CC*CCyrs*Spring precip	-0.003***	-0.005***
	(-0.001)	(-0.001)
n (unique fields)	120258	108921
N (total observations)	426055	375121
R^2	0.21	0.11
F Statistic	10256.90***	4020.34***
	(df = 8; 305789)	(df = 8; 266192)
Note:	*p<0.05; **p<0.01; ***p<0.001	

4.4 Discussion

4.4.1 Crop diversification trends

The crop diversification patterns shown in Figures 4-2 and 4-3, where the corn datasets contain more alfalfa and less winter wheat observations compared to the soybean datasets, reflect that a common diverse rotation in the Midwest is corn with alfalfa, while another is corn-soy-wheat. That cover crops were the most frequently occurring winter cover class, aside from bare and low biomass, aligns with recent work indicating that cover crops are rapidly gaining traction as a diversification practice in Michigan, and the Midwest more broadly (Surdoval et al. 2024; Seifert et al., 2018; Zhou et al., 2022). Our remote sensing dataset also confirms at a large spatiotemporal scale what previous studies have reported – that crop diversification is most common on fields with the lowest production potential (Table S4-5) (Blesh & Drinkwater, 2013; Blesh & Wolf, 2014; Seifert et al., 2018; Socolar et al., 2021). Specifically, fields with the lower mean yields, NCCPI, and field size tended to have more years of cover crops and higher RC. This underscores the importance of our modelling approach using panel fixed effects regressions, and site covariates in the linear regressions, to better control for such factors that could otherwise create downward bias for the effects of crop diversification on climate resilience.

4.4.2 Crop diversification increases yields

We found robust evidence that diversified crop rotations increase corn and soybean yields (Figure 4-4). The strong, positive effect of RC on soybean yield aligns with evidence from field experiments showing that adding small grains like winter wheat into rotation can have direct benefits for soybean productivity (Agomoh et al., 2021; Gaudin et al., 2015; Gaudin et al., 2015b; Janovicek et al., 2021). Higher prevalence of winter wheat in the soybean yield dataset compared to the corn dataset also suggests that a synergistic effect of rotation diversity may be at play. Integrating winter wheat into rotation creates an ideal window for overwintering cover crops because farmers have more time to plant a cover crop following small grain harvest in late summer than after corn or soybean harvest in late fall. The longer cover crop growing window following winter wheat allows for substantial cover crop biomass to accumulate, which then builds more SOM and increases yields (Sutton & Blesh, in prep; Sustainable Food Lab & Practical Farmers of Iowa, 2023).

The weaker effect of RC on corn yield compared to soybean (Figure 4-4) was somewhat unexpected given that alfalfa was well represented in the corn yield dataset and has known soil quality benefits (King et al., 2020; Sanford et al., 2021). In field experiments, the positive effect of crop rotation diversity on corn yield has largely been attributed to greater presence of legumes, like alfalfa and red clover, that increase SOM and meet the high N demands of corn (Gaudin et al., 2013; Gaudin, Janovicek, et al., 2015). While our panel fixed effects regressions control for time invariant factors, they do not account for changes in nutrient management that may have influenced yields, especially for corn (Smith et al., 2023). As farmers diversify their rotations, they may reduce N fertilizer inputs and rely more on ecological functions to support yields, such as N supply from legumes, which can lead to lower yields, despite potential for greater economic and environmental sustainability (Blesh & Drinkwater, 2013). Higher diversity crop rotations were also most common in the lowest fertility fields (Table S4-5), where farmers may apply less N fertilizer compared to their most productive fields where return on investment is greater (Basso et al., 2019). These factors may together underlie the weaker relationship between RC and corn yield relative to soybean.

Compared to RC, cover crop legacy effects showed even larger potential to increase corn and soybean yields, particularly for fields with at least three years of cover crops, indicating that tangible cover crop benefits take several years to accrue on working farms (Blesh, 2019; Cates et al., 2019; Nyabami et al., 2024; Wood & Bowman, 2021). In those fields, each year of cover crop use corresponded with 1.5% and 1.0% higher yields for corn and soybean (Figure 4-4), respectively, which translates to a 9% and 6% increase after six years of cover crops. In contrast, the RC models indicated that two cycles of a corn-soy-wheat rotation with cover crops corresponded with a 1.5% increase in corn yield and 4.6% increase for soybean compared to continuous monocultures of either crop. This suggests that increasing continuous living crop cover, rather than crop rotation diversity per se, may have a stronger impact on agroecosystem function (Garland et al. 2021). It is unlikely that yields can increase indefinitely, though; further research with longer-term data is needed to identify at what point yield benefits from these practices taper off.

Although cover crop legacy effects on yield were positive, immediate effects were negative overall, possibly because the most popular cover crop in the region is cereal rye (CTIC-SARE-ASTA, 2023). As an overwintering annual grass, cereal rye can rapidly accumulate biomass in the spring, which reduces nutrient losses, but can also pose preemptive competition for water and nutrients, or cause nutrient immobilization, depending on environmental conditions and growth stage at termination (Hunter et al., 2021). These negative effects can be mitigated with adaptive management, such as by adjusting the timing of cover crop termination and primary crop planting given site-specific conditions (Alonso-Ayuso et al., 2014; Balkcom et al., 2015; Rosa et al., 2021). Legume-based cover crop mixtures are more likely to have neutral or positive immediate effects on cash crop yields (Hunter et al., 2019; Ogilvie et al., 2019), and may even enhance long-term yield benefits by promoting greater microbial activity and SOM accumulation (Drinkwater et al., 1998), but we were unable to distinguish between different cover crop types in this analysis.

4.4.3 Crop diversification effects on yield stability are mixed

Contrary to our expectations, we found a negative relationship between RC and yield stability for both crops. We suspect this may be driven by several factors, including management practices that were undetectable with our remote sensing approach. Farmers with diversified systems often manage for multiple functions beyond yield, such that maximizing yields with external inputs (e.g., fertilizer and pesticides) is no longer the main goal (Rasmussen et al., 2024). These farmers may be more willing to accept inter-annual variability in field-scale crop yields because they likely have a more diverse set of crops growing at the farm-scale that buffers against variation in weather and markets (Blesh & Wolf, 2014). Additionally, the relatively short temporal scale of our dataset (12 years) compared to long-term field experiments (e.g., ranging from 10 to 30 years) may have constrained our ability to detect positive effects of RC on yield stability because it may take several crop rotation cycles for significant changes to appear (Smith et al., 2023). The fact that calculating yield stability required at least three years of yield observations also means that the highest diversity fields were underrepresented in our analyses, potentially creating downward bias in our results.

Although years of cover crop use was associated with lower yield stability in fields with less than three years of cover crops, the relationship became positive for soybean and neutral for corn in fields with three or more years of cover crops. This suggests that in early years of cover crop adoption, farmers may experience more variable yields as they gain management experience and fields reach new steady states, and highlights the importance of technical and financial support during this period (Surdoval et al., 2024). In fields with 3+ years of cover crops, soybean showed a slightly stronger yield stability response to CC years than corn, potentially due to functional differences between the two species. Corn is highly sensitive to drought, and this sensitivity has increased over time with the introduction of high-yielding varieties (Lobell et al. 2014, 2020); this trend may have therefore dampened any positive cover crop legacy effects on corn yield stability (Sanford et al., 2021). It is possible that a longer-term dataset with greater representation of fields with continuous cover cropping would continue moving the relationship between corn yield stability in a positive direction. Finally, the higher prevalence of winter wheat in the soybean yield stability dataset may be associated with higher biomass cover crops compared to the corn yield stability dataset, which could produce stronger soil quality benefits over time, and thus a stronger yield stability response.

4.4.4 Cover crop legacy effects increase planting date resilience to heavy rainfall

Our hypothesis that cover crop legacy effects would reduce planting delays under heavy spring rainfall was supported, especially for corn (Figure 4-5). We attribute the stronger effect for corn compared to soybean to the fact that corn is typically planted earlier in the spring than soybean, making corn planting date more susceptible to delays from heavy rainfall. Given that planting delays were reduced with each year of prior cover crop use, this suggests that cover crops are significantly improving soil water infiltration and retention over time (Basche et al., 2016; Basche & DeLonge, 2019). Indeed, a recent analysis found that areas with higher cover crop adoption have fewer prevented planting losses, suggesting cover crops may be a key risk reduction strategy (Won et al., 2021). When widespread floods hit the U.S. Midwest in spring 2019, qualitative evidence from a national farmer survey indicated that cover crops allowed for earlier planting than would have been otherwise possible (CTIC-SARE-ASTA, 2020).

We found that the effect of a cover crop growing in the spring immediately prior to cash crop planting was moderated by years of past cover crop use. Specifically, when a cover crop appeared in a field for the first time, planting delays were larger under heavy rainfall than if left bare, suggesting that lack of experience with cover crops can exacerbate planting delays as rainfall increases. However, after six years of cover crops, both current and past cover crop use had significant and positive effects, potentially because improved soil quality from past cover crop use enhances growth of the current cover crop, which then results in greater water uptake into and transpiration from the cover crop. Positive feedbacks such as this may enhance crop diversification benefits over time (Blesh, 2019).

Interestingly, under dry spring conditions, fields were planted later with each year of prior cover crop use, regardless of whether there was a cover crop currently growing in the field. This may be because farmers with diversified systems are more likely to use adaptive management, such as waiting until the right weather conditions arrive for planting (e.g., a rain shower shortly after planting) (Petersen-Rockney et al. 2021). More frequent cover crop use could also correspond with use of crop varieties with later planting date requirements, such as in systems transitioning to organic management, or higher cover crop biomass goals with more experience. This also helps explain why, under average precipitation, we found later primary crop planting dates as years of cover crop use increased. Additionally, cover crops grown immediately prior to primary crop planting were associated with relatively small planting delays for corn (2.68 days on average), and no significant delays for soybean. Together these findings may promote greater cover crop adoption by reducing concerns that cover crops interfere with primary crop planting (Myers & Wilson, 2023; Myers & Watts, 2015; Surdoval et al., 2024), and showing instead that they are a crucial tool for minimizing risk from increasingly variable and extreme climatic conditions.

4.5 Conclusion

Our results show that crop diversification is associated with increased corn and soybean yields in Michigan, but effects on yield stability were mixed, with cover crops showing more promise for improving yield stability than overall rotation complexity. A longer history of cover crop use also reduced plating delays under heavy spring rainfall. While numerous analyses of field station experiments have reported positive effects of crop rotation diversity on agroecosystem resilience (Bowles et al., 2020; Costa et al., 2024; Degani et al., 2019; Gaudin et al., 2013; Gaudin, Tolhurst, et al., 2015b, 2015b; Li et al., 2019; Marini et al., 2020; Sanford et al., 2021), our analysis of outcomes on working farms reveals that diversifying rotations specifically with winter cover crops may be particularly important. However, cover crop benefits can take several years to accrue, highlighting a need for incentive programs that provide technical and financial support during the early stages of transitions to more diversified systems as farmers gain experience and wait for tangible benefits (Surdoval et al., 2024). Our comparison of immediate versus legacy cover crop effects revealed there are also short-term trade-offs for primary crop yield and planting date, which necessitates concerted efforts to convey the need for long-term use to build resilience.

Although the effects of rotation complexity were generally weaker than that of cover crops, diversifying crop rotations with multiple cash crops has numerous other environmental, social, and economic benefits (Rasmussen et al., 2024; Yang et al., 2024), and is also synergistic with increasing use of cover crops. However, given that the effects of diversification on the highest fertility soils are less certain (Smith et al. 2023), changes in policy and market conditions may be necessary to facilitation crop diversification on fields with higher productivity potential. We recommend further research on working farms over longer time periods to better understand patterns and outcomes of crop rotation diversity in distinct contexts. On-farm experimentation in partnership with farmers may offer an especially useful complement to remote sensing approaches because it can reveal the role of management in driving resilience outcomes. In sum, this study provides crucial evidence from real farms that, even within several years, crop diversification builds agroecosystem climate resilience.

4.6 Bibliography

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4.7 Supplemental Material

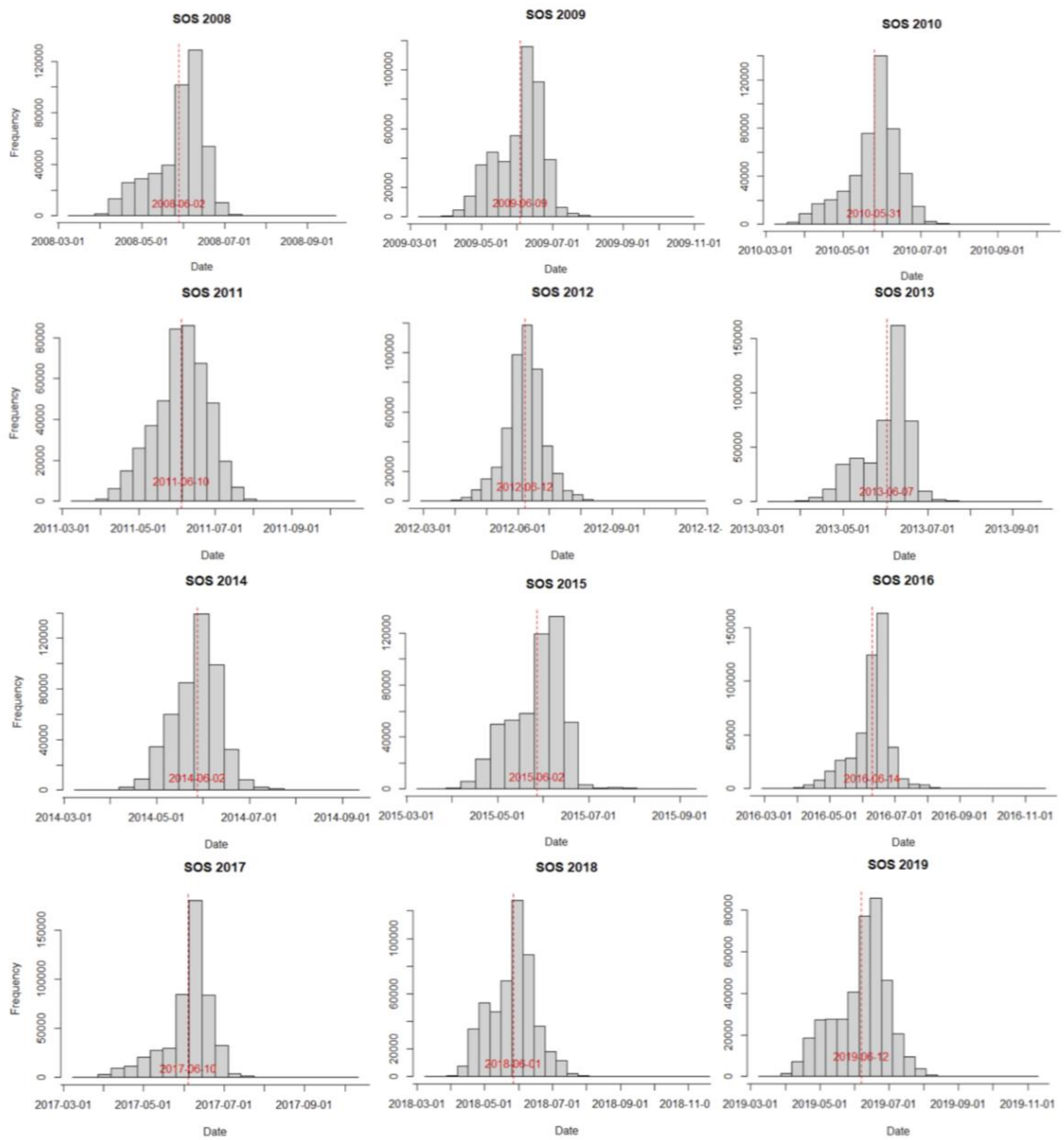

Figure 4-6: Histograms of start of season (SOS) data for corn and soybean from 2008 to 2019 derived using TIMESAT. The mean sowing date is reported in red.

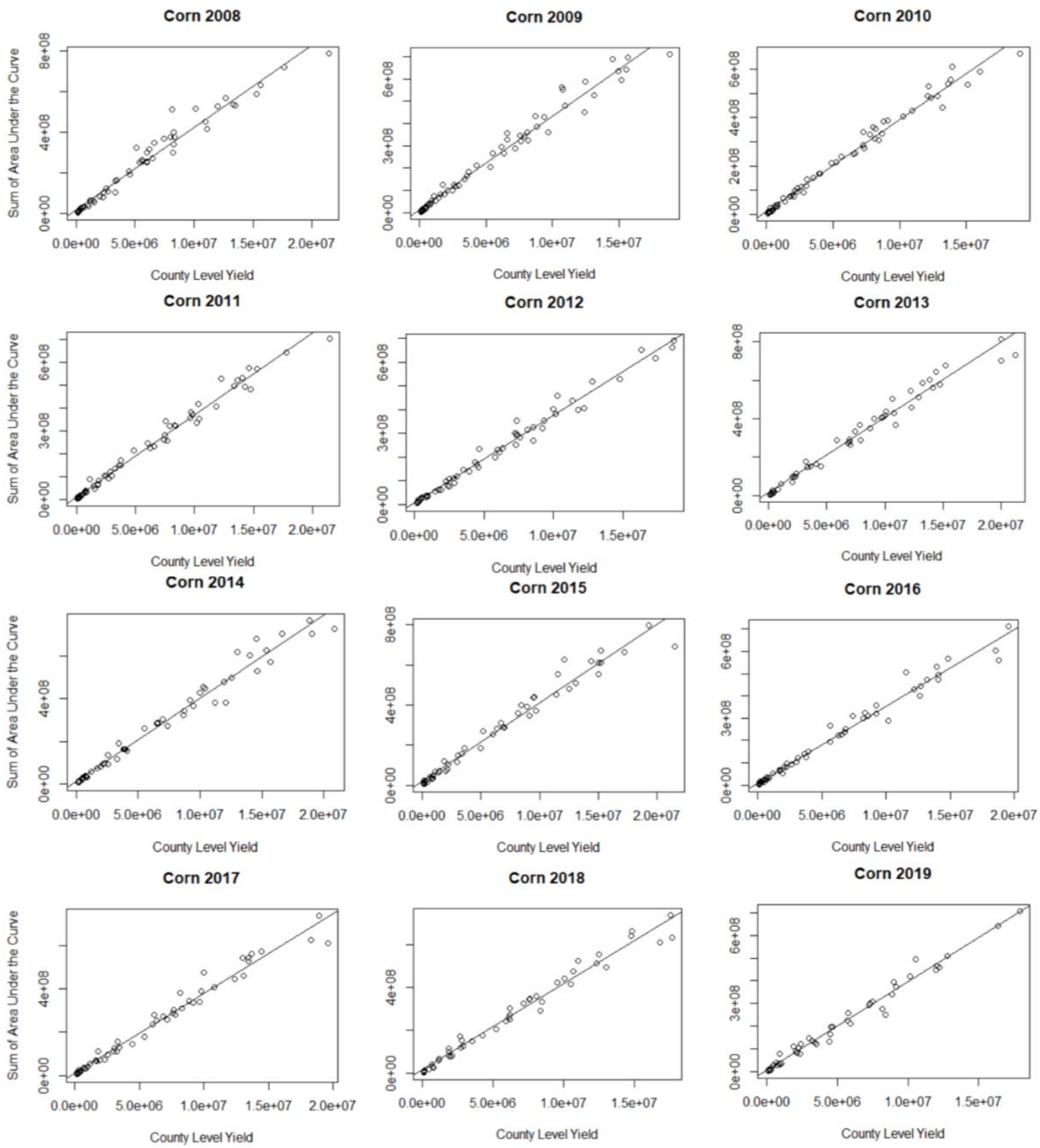

Figure 4-7: Scatterplot showing the sum of the area under the curve for corn yields derived using TIMESAT versus county-level yield from USDA NASS Quick Stats for 2008 to 2019.

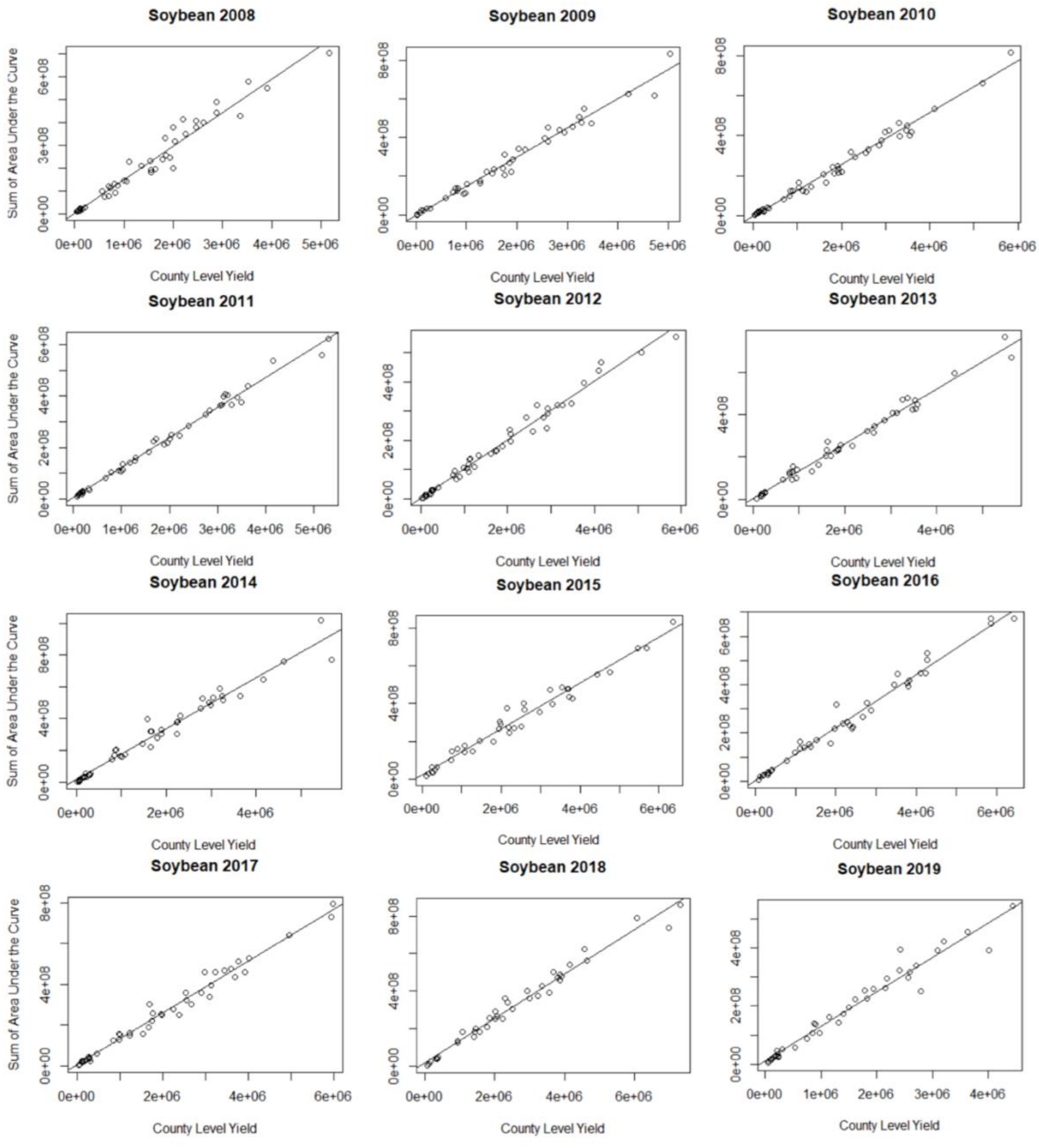

Figure 4-8: Scatterplot showing the sum of the area under the curve for soybean yields derived using TIMESAT versus county-level yield from USDA NASS Quick Stats for 2008 to 2019.

Table 4-4: Means and standard deviations for years of cover crop use and rotation complexity across the yield and yield stability datasets for corn and soybean.

Diversification practice	Full dataset	Corn yield dataset	Corn yield stability dataset	Soy yield dataset	Soy yield stability dataset
Years of cover crop	1.78	1.72	1.36	1.76	1.38
	(2.35)	(2.31)	(1.99)	(2.35)	(2.05)
Rotation complexity	5.15	5.19	4.79	5.20	4.77
	(2.1)	(2.43)	(1.9)	(2.38)	(1.7)
N (fields)	144,138	136,653	92,017	125,680	81,872

Table 4-5: Means for crop yield, years of cover crop use (CC years), rotational complexity (RC), soil quality (NCCPI), and field size for ten yield quantiles for corn (top) and soybeans (bottom). NCCPI = National Commodity Crop Productivity Index.

CORN					
Yield quantile	**Yield (Mg ha^{-1})**	**CC years**	**RC**	**NCCPI**	**Field size (ha)**
0.1	5.97	2.84	5.05	565	14.7
0.2	6.04	2.18	4.87	572	17.7
0.3	6.55	1.84	4.82	577	18.7
0.4	6.94	1.55	4.76	581	19.5
0.5	7.28	1.29	4.71	585	20.2
0.6	7.60	1.12	4.70	585	20.9
0.7	7.91	0.93	4.70	586	21.7
0.8	8.23	0.80	4.70	587	22.8
0.9	8.62	0.59	4.65	589	23.8
1	9.35	0.42	4.96	585	25.2
SOYBEAN					
Yield quantile	**Yield (Mg ha^{-1})**	**CC years**	**RC**	**NCCPI**	**Field size (ha)**
0.1	1.48	2.76	5.08	594	12.8
0.2	1.80	2.14	4.91	594	15.7
0.3	1.95	1.74	4.81	593	17.5
0.4	2.05	1.42	4.81	597	19.1
0.5	2.14	1.27	4.76	594	20.1
0.6	2.23	1.12	4.73	595	20.6
0.7	2.31	0.98	4.68	595	21.4
0.8	2.40	0.90	4.62	595	22.3
0.9	2.51	0.79	4.62	596	23.1
1	2.71	0.70	4.65	594	23.1

Chapter 5 – Conclusion

Using an integrative approach to study crop diversification practices on working farms, this dissertation showcases that action-oriented and participatory research is key to advancing food system sustainability and resilience. Chapters 2 and 3 leverage researcher-practitioner partnerships to uncover interactions between site-specific conditions and crop diversification outcomes, first through an experiment using a functional trait-based approach, and then with citizen science comparing performance of different cover crop types. Analysis of remote sensing data in Chapter 4 reveals that increasing crop rotation diversity with cover crops increases climate resilience on working farms. The work presented here thus applies ecological science to agricultural research to address gaps in our knowledge of how to manage agroecosystem diversity for multiple benefits in real-world farming contexts.

5.1 Key takeaways: Crop diversity across ecological, spatial, and temporal scales

The three studies in this dissertation bring together principles of functional, community, and ecosystem ecology to advance knowledge of complex interactions and processes in agroecosystems. Specifically, each chapter examined how various types and levels of crop diversity perform across the heterogeneous environmental and management conditions on working farms in the Great Lakes region. In a two-year experiment on eight farms in Michigan (Chapter 2), I quantified trait variation for three functionally diverse cover crop species in response to a gradient of soil health and interspecific interactions when grown together in mixture. I found that intraspecific trait variation (i.e., variation within species) was as important as trait variation between species, and that patterns of intraspecific variation were species-specific. These results underscore that cover crop selection should not be based solely on trait differences between species, as is common practice, but also on differences in trait expression within each species across varying conditions. Because trait expression affects the functions each species supports, a refined approach to cover crop research and management that considers trait variation both within and between species will improve the prediction and realization of ecosystem services from cover crops.

Recognizing that cover crop performance can vary in response to many factors beyond those captured in the on-farm experiment, I complemented Chapter 2 with a larger-scale, observational citizen science study in Chapter 3. Although cover crop performance was highly variable across farm fields, management based on ecological principles produced the best outcomes. Specifically, cover crop biomass increased with greater cover crop species diversity. Biomass also increased when cover cropping was combined with other ecological management practices, such as increasing primary crop diversity and using organic soil amendments. I also found that interactions between management history and environmental conditions affected outcomes of other cover crop management decisions, such as planting method. This novel citizen science approach is a promising tool for monitoring cover crop performance and identifying practical and context-specific opportunities for improving management to enhance agroecosystem function.

The final study used remote sensing data to test the effects of crop diversity on climate resilience. While increasing crop rotation complexity was associated with higher yields, it did not show clear benefits for yield stability. On the other hand, increasing the functional diversity of rotations with overwintering cover crops had significant, positive effects on both yield and yield stability. Overwintering cover crops also reduced planting delays under heavy spring rainfall, providing an additional mechanism by which cover crops bolster resilience. Importantly, I distinguished between legacy and immediate cover crop effects in these analyses, showing that resilience benefits were largely driven by the number of years of past cover crop use (i.e., legacy effects). This analysis provides crucial evidence for which types of crop diversity may matter most for agroecosystem climate change adaptation on working farms.

Taken together, the three studies highlight the importance of leveraging functional diversity and systems thinking across multiple spatial and temporal scales to support positive outcomes in agroecosystems. They also underscore that research situated within real-world farming conditions is critical for identifying context-dependent relationships.

5.2 Lessons from research on working farms

5.2.1 Translating research into action

Beyond advancing scientific understanding of complex agroecological dynamics, research on working farms can help fuel food system transformation. Despite several decades of evidence from field station, greenhouse, and laboratory experiments that increasing crop diversity promotes critical agroecosystem functions, adoption of diversification practices remains low. There are indeed major structural barriers hindering transitions to diversified systems (Stuart & Gillon, 2013), but there is also a growing body of literature identifying key factors that assist farmers in overcoming those barriers (Blesh et al., 2023). Throughout my dissertation research, I aimed to use methods that recognize and integrate these mobilizing factors to maximize potential for translating research into action.

At local scales, successful diversification requires place-based knowledge of the types of species, practices, and management approaches that work best for a given set of conditions. The on-farm experiment and citizen science study directly address this need by collecting detailed data from real farms that can inform actionable and site-specific management recommendations. Because farmers often cite the experience and advice of other farmers as one of their most trusted sources of information (Asprooth et al., 2023), gathering and analyzing data from working farms also lends credence and relevance to the findings of this dissertation. For instance, the results of the climate resilience analysis in Chapter 4 may be more compelling to farmers than those from field station experiments because they are based on data from real farms. Evidence that farmers have been successfully using diversification practices can then motivate other farmers to try new practices (Han & Niles, 2023; Rogers et al., 2008).

At regional scales, farmer networks have been identified as a key factor driving adoption of agroecological practices (Baumgart-Getz et al., 2012; Bressler et al., 2021). Farmer networks facilitate the exchange of knowledge and ideas and create new social norms that favor diversification practices. Over 100 farmers from across the Great Lakes region were direct collaborators in this dissertation research, creating a rich network with a shared goal of advancing agroecological research and practice. These farmers were invited to engage with each other, and with conservation professionals, members of state and local agencies, and researchers during field days, webinars, and interactive presentations. These outreach activities fostered meaningful relationships and collective learning to bolster agricultural sustainability and resilience in the region.

The intentional integration of outreach activities as part of this dissertation research was also critical for learning with and from the agricultural community. Too often, research takes place in academic silos, limiting its potential to effect positive change. By partnering with farmers in this research, regularly communicating research progress, and inviting their feedback and ideas, I was able to develop and implement research that is well-aligned with the needs of the agricultural community and better positioned to inform action. Farmers also have intimate knowledge of their land and management practices, such that they were able to offer invaluable insights about research findings, further highlighting the value of research co-production. This underscores the importance of blending diverse forms of agroecological knowledge (Blesh & Schipanski, 2024). Of course, the durability of these relationships hinges upon trust and reciprocity. Farmers were much more willing to partner in research when they knew they would receive useful information in return for their time, data, and ideas. As such, prioritizing timely delivery of data and research updates was critical in building and maintaining these researcher-practitioner partnerships.

5.2.2 Policy and program implications

The findings of this dissertation research have several important implications for agricultural policy and conservation programs. First, the fact that cover crop performance was context-dependent and suboptimal on many fields highlights a need for place-based technical assistance informed by site-specific conditions. This assistance could be delivered through local conservation districts, extension agents, or certified crop advisors, but should be guided by a foundational knowledge of the ecological principles and interactions governing outcomes in agroecosystems. Each agroecosystem contains a unique and interacting suite of environmental and management variables; basing conservation policies and programs on ecological knowledge and systems thinking is therefore essential for catalyzing successful transitions to diversified systems that support multiple ecosystem services. Accordingly, there should also be concerted efforts to integrate more agroecological education into training for agricultural professionals.

Second, the field assessment protocol developed for the citizen science study could be used to increase the effectiveness of agricultural conservation programs. Most programs are currently based on presence or absence of conservation practices like cover cropping, but as shown in the citizen science study, the actual performance of these practices can vary widely. Instead, programs should focus on optimizing outcomes. In the case of cover crops, farmers could be compensated based on the level of biomass they achieve, which can be easily estimated using the field assessment protocol. Alternatively, the citizen science approach could be used to develop management guidelines that are linked to improved outcomes, such as increasing the diversity of primary crops and cover crops, or making sure that cover crops reach a threshold level of growing degree days. However, the citizen science study also revealed that there are many paths to the same destination; a "one-size fits all" approach to conservation programs can thus be too confining, and care should be taken to allow room for innovative and adaptive management.

Third, evidence from the climate resilience analysis that it can take several years before tangible benefits appear after implementing diversification practices highlights a need for cost-share programs during early years of transitions to diversified systems. This would reduce risk for those considering adoption, especially given that there may be short-term tradeoffs as farmers gain experience and fields reach new steady states. A recent analysis of the federal Environmental Quality Incentives Program (EQIP) supports and expands on this idea based on qualitative evidence from farmer interviews (Surdoval et al., 2024). They recommend financial support for farmers to experiment with new practices at small scales while gaining experience; allowing more flexible management approaches; and extending the duration of contracts to better match the timeframes necessary for restoring agroecosystem functions. This dissertation presents complementary quantitative evidence that farmers' assessments of policy and program needs are well aligned with the agroecological outcomes occurring in their fields.

5.3 Future directions

In general, there is a need for more research on working farms that builds on the methods, concepts, and findings presented here. The trait-based approached used in the on-farm experiment could be applied to new locations and management systems to develop a more mechanistic and generalizable understanding of relationships between the diverse biotic and abiotic conditions on real farms. Similarly, the citizen science framework could be applied to new regions and contexts to monitor performance of crop diversification practices across large spatial and temporal scales. Expanding the cover crop citizen science dataset would enable analysis of additional cover crop species across a broader suite of farming systems, or addressing more nuanced questions, such as which management practices work best in specific soil types. This type of research can then inform decision support tools to optimize outcomes.

To continue advancing understanding of relationships between crop diversification and climate resilience on working farms, there is a need for longer-term datasets, either through remote sensing, collaborative on-farm research, or both. This would allow for better detecting the effects of crop rotation diversity on yield stability, both of which are best measured over multiple decades. It would also be useful to expand resilience analyses to different scales (e.g., resilience at farm, community, and national-scales) (Renard & Tilman, 2019; Sundstrom et al., 2023), and in consideration of a broader suite of ecological and social resilience indicators. For instance, although rotation complexity was not associated with greater field-scale temporal yield stability for corn and soybean in my analysis, diversified rotations could increase farm-scale resilience from year-to-year because having multiple crops increases the chance that at least a few will do well in a given year. It can also provide greater economic resilience when farmers are able to reduce reliance on external inputs with volatile prices and instead rely on ecological functions and processes to support crop production.

Finally, there are exciting opportunities to blend the three approaches used in this dissertation to harness their strengths while mitigating their respective weaknesses. Identifying easily-measurable proxies for outcomes of interest, as in the citizen science study, could allow for expanding on-farm experiments to a larger number of farms and locations. Based on the enthusiasm with which much of this dissertation research was met, there are likely many farmers who would be excited to test specific crop diversification treatments on their farms and help gather data as long as it is not too onerous and they receive useful information in return. This could allow for better discerning cause-and-effect than in a purely observational setting, while also expanding on-farm experiments beyond the scale at which they are typically feasible. Remote sensing could also make long-term, on-farm experiments more feasible if it can be used to monitor outcomes over time (e.g., yield) such that less time and labor is required for maintaining these experiments. On the other hand, given that the remote sensing analysis here was limited by lack of management information, pairing management surveys like the one disseminated for the citizen science study with remote sensing analyses could greatly expand the types of questions that can be addressed (Hively et al., 2009).

In closing, the time is ripe for leveraging innovative and collaborative approaches to agroecological research that embrace real-world variability in environmental and management conditions in agricultural landscapes. This dissertation provides strong evidence that increasing the functional diversity of crop rotations, particularly with cover crops, is crucial for fostering positive ecological interactions and outcomes in agroecosystems, especially when combined with other agroecological practices. It also sheds light on the complexity of agroecosystems, in which current and past management decisions interact with plants and soils to influence ecological functions and processes. Continued research merging ecological principles and theory with agricultural systems across multiple spatial, temporal, and organismal scales is key to building a more sustainable and resilient food system.

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Appendices

Appendix A: Field Assessment for Cover Crop Citizen Science Study (Chapter 3)

Citizen Science for Great Lakes Cover Crops (Single-species) Date: _____________

Farm ID: ____________________________________

Field ID: ______________________________________

(these IDs should be the same as what you submitted in the Farm & Management survey)

Instructions:

1. Navigate to your cover crop field and **take a photo** of the entire field.

2. **Rate the level of patchiness** of the cover crops across the entire field (1 = not patchy at all; 3 = half bare soil, half cover crop; 5 = extremely patchy):
   1 2 3 4 5

3. Next, navigate to a location in your field with **average** cover crop growth, making sure to avoid field edges.

4. Holding your arm out parallel to the ground, **take a photo of the *cover crop canopy***. The photo should be directly overlooking the cover crops, like an aerial photo (i.e., NOT at an angle). Make sure to avoid capturing any shadows, shoes, or other objects in the photo.

5. In the space provided on the next page, **rate the amount of weed pressure** on a scale of 1 to 5, and collect **height measurements** for three average cover crop plants.

6. Repeat steps 3-5 at two more locations in your field.

7. When you are finished with your field assessment, take a picture of (or scan) these data sheets, and send them, along with your cover crop canopy photos, to herricke@umich.edu.

What cover crop species are you collecting measurements for?

____

Circle the unit of your height measurements: *inches* *centimeters*

<u>Sampling location #1</u>

Weed pressure (1 = very low; 3 = half weed/half cover crop biomass; 5 = very strong):

1 2 3 4 5

Height measurements:
Plant 1: _____________
Plant 2: _____________
Plant 3: _____________

<u>Sampling location #2</u>

Weed pressure (1 = very low; 3 = half weed/half cover crop biomass; 5 = very strong):

1 2 3 4 5

Height measurements:
Plant 1: _____________
Plant 2: _____________
Plant 3: _____________

<u>Sampling location #3</u>

Weed pressure (1 = very low; 3 = half weed/half cover crop biomass; 5 = very strong):

1 2 3 4 5

Height measurements:
Plant 1: _____________
Plant 2: _____________
Plant 3: _____________

Citizen Science for Great Lakes Cover Crops (Mixture) Date: ____________________

Farm Name: ____________________________________

Field ID: ______________________________________

(the Field ID should be the same as what you submitted in the Farm & Management survey)

<u>Instructions:</u>

1. Navigate to your cover crop field and take a photo of the entire field.

2. Rate the level of patchiness of the cover crop across the entire field (1 = not patchy at all; 3 = half bare soil, half cover crop; 5 = extremely patchy):

   1 2 3 4 5

3. Circle the unit you will record your height measurements in: *inches* *centimeters*

4. Next, navigate to a location in your field with **average** cover crop growth, making sure to avoid field edges.

5. On the next page, assign each overwintering species in your mixture a number and visually estimate their relative proportions (for example, Species 1 = 75%, Species 2 = 25%). If your mixture contains more than four species, list the four most dominant species.

6. Holding your arm out parallel to the ground, **take a photo of the *cover crop canopy***. The photo should be directly overlooking the cover crops, like an aerial photo (i.e., NOT at an angle). Make sure to avoid capturing any shadows, shoes, or other objects in the photo.

7. In the space provided on the next page, rate the amount of **weed pressure** at this location on a scale of 1 to 5.

8. Collect and record **three height measurements for each cover crop species** in your mixture (or the four most dominant species if more than a four-species mixture), *making sure the height measurements are recorded under the correct species number* assigned in step 5.

9. Repeat steps 4-8 at two more locations in your field.

10. When you are finished with your field assessment, take a picture of (or scan) these data sheets, and send them, along with your cover crop photos, to herricke@umich.edu.

Sampling location #1

Species 1: ________________________ *% of mixture:* ________ *Species 3:* ________________________ *% of mixture:* ________
Species 2: ________________________ *% of mixture:* ________ *Species 4:* ________________________ *% of mixture:* ________

Weed pressure (1 = very low; 3 = half weed/half cover crop biomass; 5 = very strong): 1 2 3 4 5

Height Measurements

Species 1			Species 2			Species 3			Species 4		

Sampling location #2

Species 1: ________________________ *% of mixture:* ________ *Species 3:* ________________________ *% of mixture:* ________
Species 2: ________________________ *% of mixture:* ________ *Species 4:* ________________________ *% of mixture:* ________

Weed pressure (1 = very low; 3 = half weed/half cover crop biomass; 5 = very strong): 1 2 3 4 5

Height Measurements

Species 1			Species 2			Species 3			Species 4		

Sampling location #3

Species 1: ________________________ *% of mixture:* ________ *Species 3:* ________________________ *% of mixture:* ________
Species 2: ________________________ *% of mixture:* ________ *Species 4:* ________________________ *% of mixture:* ________

Weed pressure (1 = very low; 3 = half weed/half cover crop biomass; 5 = very strong): 1 2 3 4 5

Height Measurements

Species 1			Species 2			Species 3			Species 4		

Appendix B: Farm & Management Questionnaire for Cover Crop Citizen Science Study (Chapter 3)

Citizen Science for Great Lakes Cover Crops – Farm & Management Questionnaire

Thank you for partnering with us to better understand cover crop performance across the Great Lakes region! Your participation will help us improve recommendations for cover crop management.

This survey asks questions about different aspects of your cover crop field and management practices, and should take roughly 15-20 minutes to complete. Note that if you plan to report data for multiple cover crop fields, you will need to complete a **separate survey for each field**. After submitting this survey you will receive instructions for completing the field assessment in the spring prior to cover crop termination. All information you report in this survey will be kept confidential. Contact herricke@umich.edu with any questions.

Participant name:

Email address:

Phone number:

Postal address you would like your participation payment sent to:

Name of your farm:

Name/ID for your cover crop field (use something you can easily remember - you'll be asked to use this ID again for the field assessment):

Please answer the following questions specifically for the field you listed in the previous question.

1. Where is your cover crop field located?
    a. State:
    b. County:
    c. Zipcode:

2. How many years has this land been used for agricultural purposes?
    a. 0-5
    b. 6-10
    c. 11-24
    d. 25-49 *(skip to question 4)*
    e. More than 50 years *(skip to question 4)*
    f. Unsure

3. Which of the following best describes this land prior to its use as an agricultural field?
    a. Grassland/prairie
    b. Shrubland
    c. Forest (deciduous)
    d. Forest (coniferous)
    e. Forest (mixed)
    f. Wetland
    g. Residential lawn
    h. It has been in cultivation for as long as I can remember
    i. I don't know
    j. Other ____________________

4. What type of farming is this field currently used for (e.g., row crops, perennial pasture, organic vegetable farm, etc.)? Please describe below.

    a. How many years have you used this field for that type of farming?
        i. 0-2
        ii. 3-5
        iii. 6-10
        iv. 11-15 *(skip to question 6)*
        v. 15-20 *(skip to question 6)*
        vi. 21+ *(skip to question 6)*

5. Has this field been used for any other types of farming (e.g., row crop production, perennial pasture, organic vegetable farm, etc.) prior to its current use? Please describe below.

    a. How many years was this field used for that type of farming?
        i. 1-5
        ii. 6-10
        iii. 11-15

            iv. 15-20
            v. 21+

6. Which soil type best describes this field?
    a. Sand
    b. Sandy loam
    c. Loam
    d. Silt loam
    e. Clay loam
    f. Clay
    g. Unsure

7. What is the dominant soil series for this field?

8. Which of the following best describes the topography of this field?
    a. Mostly flat
    b. Gentle slopes (2-6%)
    c. Moderate slopes (6-12%)
    d. Steep slopes (greater than 12%)

9. Do you ever observe standing water on the field for prolonged periods of time following heavy rainfall?

    a. Yes – often
        i. On how much of the field?
            1. <25%
            2. 26-50%
            3. 51-75%
            4. 76-100%

    b. Yes – occasionally
        i. On how much of the field?
            1. <25%
            2. 26-50%
            3. 51-75%
            4. 76-100%

    c. No

10. Does this field have issues retaining water, or become undesirably dry during an **average** growing season?
    a. Yes – often
    b. Yes – occasionally
    c. No

11. What is your biggest management challenge in this specific field?

12. What type(s) of tillage have you used in this field in the past five years? Select all that apply.

	Conventional tillage	Reduced tillage	No-till	Other
2022				
2021				
2020				
2019				
2018				

If you selected “Other” above, how would you describe your tillage practices?

a. Prior to the past five years, what type of tillage did you typically use on this field?
    i. Conventional tillage
    ii. Reduced tillage
    iii. No-till
    iv. Other ________________

13. How many months out of the year does this field typically have living soil cover? This includes cover crops, cash crops, or any other type of plant cover you might include in your rotations.
    a. 1-4
    b. 5-7
    c. 8-10
    d. 11-12

14. What has the cash crop rotation been for this field over the past five years? If you at any point had multiple cash crops growing in this field at the same time or in the same year, please answer considering the dominant cash crop in the portion of the field where you plan to sample your cover crops for the field assessment.

Year	Cash crop
2022	
2021	
2020	
2019	
2018	

15. Have you applied compost to this field in the past ten years? Yes No

If Yes…

How frequently do you apply compost to this field?

1. Multiple times a year
2. Once a year
3. Every other year
4. Every few years
5. Less than every few years

16. Have you applied manure to this field in the past ten years? Yes No

If Yes…

How frequently do you apply manure to this field?

1. Multiple times a year
2. Once a year
3. Every other year
4. Every few years
5. Less than every few years

What time of year do you typically apply manure?

1. Spring
2. fall

17. How long have you been using cover crops in this field?
    a. This is my first year using cover crops in this field (*skip to question 22*)
    b. 2-5 years
    c. 6-10 years
    d. 11-20 years

e. More than 20 years

18. How frequently do you use cover crops in this field?
    a. Every year
    b. Every other year
    c. Every 3-4 years
    d. Less than every 4 years
    e. Other _______________

19. How often do you use each of the following types of cover crops in this field?
    a. Grasses (e.g., cereal rye, oats)
        i. Every year
        ii. Every other year
        iii. Every few years
        iv. Less than every few years
        v. Never
    b. Legumes (e.g., clovers, hairy vetch)
        i. Every year
        ii. Every other year
        iii. Every few years
        iv. Less than every few years
        v. Never
    c. Brassicas (e.g., mustard, radish)
        i. Every year
        ii. Every other year
        iii. Every few years
        iv. Less than every few years
        v. Never
    d. Broadleaf (e.g., buckwheat)
        i. Every year
        ii. Every other year
        iii. Every few years
        iv. Less than every few years
        v. Never
    e. Other (please describe ________________________)
        i. Every year
        ii. Every other year
        iii. Every few years
        iv. Less than every few years

20. Do you typically plant single-species cover crops or cover crop mixtures in this field?

    a. Single-species cover crops
    b. Cover crop mixtures

i. How many cover crop species do you typically include in a mixture for this field?
    1. 2-4
    2. 5-10
    3. 11-14
    4. 15+

ii. What types of cover crops do you grow together in your mixtures? Select all that apply.
    1. Grasses
    2. Legumes
    3. Brassicas
    4. Other ____________________

21. Is there anything else you'd like us to know about your experience or goals managing cover crops in this field?

22. What type of cover crop is currently growing in this field?
    a. Single-species
        i. What cover crop species are you growing?

        ii. What was the cover crop seeding rate (lbs/ac)?

    b. Mixture
        i. List all the overwintering species in your mixture:

        ii. What were their seeding rates (lbs/ac)? Please list seeding rates for each individual species if possible.

        iii. List all the winter-kill species in your mixture:

        iv. What were their seeding rates (lbs/ac)? Please list seeding rates for each individual species if possible.

c. Did you irrigate this cover crop? Yes No

d. Has this cover crop been grazed, or do you plan to graze it?

Yes No

e. Why did you choose this particular cover crop?

f. Did you apply (or plan to apply) any of the following nutrient inputs **during the cover crop growing season** (i.e., not including any inputs applied to the previous harvested crop)?

i. Synthetic nitrogen fertilizer: Yes No

If Yes…

a. When did you apply fertilizer?

b. At what rate was the fertilizer applied? If unknown, enter the total amount applied (please include units - e.g., tons or lbs per acre).

ii. Synthetic phosphorus fertilizer: Yes No

If Yes…

a. When did you apply fertilizer?

b. At what rate was the fertilizer applied? If unknown, enter the total amount applied (please include units - e.g., tons or lbs per acre).

iii. Manure: Yes No

If Yes…

a. When did you apply manure?

b. How much manure was applied (please include units - e.g., tons or lbs per acre)?

iv. Compost: Yes No

If Yes…

a. When did you apply compost?

b. How much compost was applied (please include units - e.g., tons or lbs per acre)?

g. How did you prep this field for planting the cover crop? If the cover crop was interseeded, please note which crop it was interseeded into.

h. How was the cover crop planted?
   i. Broadcast
   ii. Drilled
   iii. Aerial (flown on)
   iv. Other ____________________

i. What date was the cover crop planted?

j. What is the total area of this field planted to the cover crop?

k. When do you plan to terminate this cover crop?

l. How do you plan to terminate this cover crop?

m. Please rate your satisfaction with this cover crop stand. (1 = very unsatisfied, 5 = very satisfied)

1 2 3 4 5

23. What crop was grown in this field immediately prior to this cover crop?

a. What was the yield (e.g., bu/ac) of the harvested crop?

b. Did you apply any of the following nutrient inputs to this crop?

   i. Synthetic nitrogen fertilizer: Yes No

      If Yes…
      a. When did you apply fertilizer?
      b. At what rate was the fertilizer applied? If unknown, enter the total amount applied (please include units - e.g., tons or lbs per acre).

   ii. Synthetic phosphorus fertilizer: Yes No

      If Yes…
      a. When did you apply fertilizer?
      b. At what rate was the fertilizer applied? If unknown, enter the total amount applied (please include units - e.g., tons or lbs per acre).

   iii. Manure: Yes No

      If Yes…
      a. When did you apply manure?
      b. How much manure was applied (please include units)?

   iv. Compost: Yes No

      If Yes…
      a. When did you apply compost?
      b. How much compost was applied (please include units)?

24. What crop do you plan to plant following the cover crop?