1 General Introduction

1.1 Motivation

The global population has reached an unprecedented size, and the demand for food continues to grow (van Dijk et al. 2021). At the same time, human activity is threatening the very conditions that sustain life, driving crises such as climate change, biodiversity loss, air and water pollution (Rezaei et al. 2023). Agriculture, while essential for food production, is also a major contributor to these environmental challenges (Ortiz et al. 2021; Yang et al. 2024). To address this, the sector seeks for solutions that enhance productivity while minimizing negative environmental impacts (Denning 2025). Among the many strategies discussed for achieving sustainable intensification in crop production, one already available and offering numerous benefits is the cultivation of cover crops (Quintarelli et al. 2022).

Cover crops are planted after the main crop is harvested, filling the fallow period before the next main crop is established. This practice is widespread after a winter crop that is followed by a spring crop, including the winter vegetation break. Their aboveground biomass covers the soil surface, protecting it from physical impacts such as rain, frost, heat, and wind. This helps prevent erosion by absorbing the energy of raindrops or wind (Blanco-Canqui et al. 2015), suppresses weed germination (Fernando & Shrestha 2023), enhances soil biology by improving the microclimate (Zibilske & Makus 2009), and reduces water loss through evaporation (Selzer & Schubert 2023). Cover crops are terminated by frost, mechanical, or chemical methods before the establishment of subsequent main crops, which can then utilize the nutrients released during litter decomposition (Langelier et al. 2021; Marcillo et al. 2024).

Belowground, a network of root biomass is formed that explores the soil to source water and nutrients, while the interaction with the edaphon marks the starting point of the soil food web. In this process, highly mobile nutrients, such as nitrate or sulfate - left as residues from the previous crop or released through soil mineralization - are effectively recovered, reducing the risk of leaching (Thapa et al. 2018). Fine root turnover and rhizodeposition feed soil biota, increasing microbial diversity and activity and positively impacting soil structure and stress resilience (Scavo et al. 2022). Soil physical properties can be improved, including penetration resistance, aggregate stability, and macroporosity (Blanco-Canqui & Ruis 2020). Root exudation of solubilizing compounds and symbiosis with arbuscular mycorrhizal fungi can mobilize otherwise unavailable nutrients such as phosphorus and metallic micronutrients (Hallama et al. 2019). In the case of leguminous species, symbiosis with rhizobia adds additional nitrogen to the system from the atmosphere through biological nitrogen fixation (De Notaris et al. 2021). Specifically bred cover crop varieties are often the only effective measure to reduce the abundance of plant-parasitic nematodes in the soil (Mushtaq et al. 2024).

In summary, cover crops can simultaneously address agronomic, environmental and societal targets. On the agronomic side, they can increase yield potential by protecting and enhancing soil fertility while reducing inputs in tillage, fertilization or weed management (Garba et al. 2024). Their potential to increase soil organic carbon stocks through atmospheric carbon sequestration contributes to mitigating global warming and climate change (Poeplau & Don 2015; Schön et al. 2024). Additionally, by reducing the risk of nutrient losses, cover crops help prevent water pollution (Blanco-Canqui 2018). Incorporating diverse plant species into crop rotations and extending the period of plant growth increases agroecosystem biodiversity and provides habitats for wildlife (Bryan et al. 2021).

The quality and quantity of these cover crop benefits, often called ecosystem services, depend on species identity, environmental impacts, and management practices, as well as the interactions among these factors (Lamichhane & Alletto 2022). Consequently, the question arises: how can cover cropping be optimized to maximize ecosystem services? While environmental factors such as soil properties and weather cannot be controlled, management practices vary by farm and farmer characteristics and should be adapted to the local conditions (Peltonen-Sainio et al. 2023). A key factor is selecting species that are well-suited to the environmental conditions and capable of delivering the desired ecosystem services (Finney et al. 2017). Cover crop species show various characteristics and functions including growth rates, nutrient acquisition, leaf and root traits, and ecological strategies (Tribouillois et al. 2015). This diversity enables adaption to a wide range of conditions and applications, provided that the individual responses of each species are well understood. In addition to selecting and cultivating single species, another approach to optimize cover cropping is combining different species into mixtures to enhance the overall benefits provided. In recent years, cover crop mixtures have gained popularity and were supported by various stakeholders, including the seed industry, science and policy (Chapagain et al. 2020).

Species richness in cover crop mixtures varies, ranging from simple two-species mixtures to complex combinations of ten or more species. Some stakeholders promote highly diverse mixtures, believing that maximizing the number of species enhances the performance and benefits of cover crops. This is often based on the diversity-productivity hypothesis, which is supported by ecological theories of niche differentiation, niche complementarity, and resource use efficiency (Brooker et al. 2015; Scherer-Lorenzen 2009; Van Ruijven & Berendse 2005). However, literature analyses have not found a clear, general trend for cover crop mixtures to outperform pure stands (Lavergne et al. 2021; Florence & McGuire 2020). Explanations for this discrepancy can be found in the fundamental differences between more natural ecosystems where these theories were developed and agriculture, which undergo anthropogeny management interventions and have relatively short vegetation periods for cover crops, limiting the effects of ecological succession (Reinhold-Hurek et al. 2024).

Nevertheless, some studies have demonstrated the overperformance of mixtures for several ecosystem services (Elhakeem et al. 2021; Heuermann et al. 2022; Gentsch et al. 2022; Wendling et al. 2017). Research has shown that combining species with functionally diverse traits enhances the multifunctionality of ecosystem services (Finney et al. 2017; Garba et al. 2024). To ensure the functionality and high performance of cover crop mixtures, combining suitable species and understanding how species complement each other within mixtures is crucial (McKenzie-Gopsill et al. 2022). As soon as individuals grow next to each other, competition for growth factors such as light, water, and nutrients begins (Craine & Dybzinski 2013). This occurs as both intraspecific and interspecific competition and can be influenced by management practices, particularly by adjusting seed rates in pure stands and also mixtures' proportions (Hauggaard-Nielsen et al. 2006). However, the effect of species identity, combination and seed rate configuration on the performance of cover crop mixtures is mainly unknown, highlighting the need for region-specific management strategies (Ruis et al. 2019).

The performance of cover crops refers to their ability to provide ecosystem services, which can be diverse and vary in importance depending on their intended purpose. Assessing all ecosystem services is challenging, so performance is often evaluated using more easily measurable indicators such as aboveground biomass, nutrient accumulation, and litter quality (Finney et al. 2016). However, evaluating these indicators requires considerable labor and financial investment for destructive sampling methods (Catchpole & Wheeler 1992). Remote-sensing approaches could offer a promising solution to facilitate and scale up the evaluation of cover crop performance, (Weiss et al. 2020). Analyzing reflectance in the visible and near-infrared spectral ranges, as well as modeling canopy volumes with height measurements using photogrammetry, have been demonstrated to be effective tools for assessing cover crop performance (Rosen et al. 2024; Holzhauser et al. 2022; Roth & Streit

2018). This can be complicated by mixtures containing species with different developmental rhythms and shoot morphologies, highlighting the need to investigate remote sensing methods to overcome these challenges for monitoring cover crop canopies.

1.2 Objectives

This thesis aims to investigate how management decisions regarding the species selection and composition of cover crops affect their provisioning of ecosystem services. This should lead to recommendations for strategies and tools to help stakeholders develop enhanced cover crop mixtures for sustainable intensification of agricultural production. The following research objectives are being pursued:

- systematically investigate the impact of different cover crop species on biomass production, weed suppression, nutrient accumulation, and litter quality under varying environmental conditions
- assess how species combination, as well as intra- and interspecific competition and facilitation, influence cover crop performance to identify optimal species combinations and seed rate configurations for mixtures
- explore interaction-based modeling approaches and remote-sensing based monitoring for predicting and monitoring cover crop performance as possible solutions to facilitate the development of cover crop mixtures

2 Publications

2.1 Improving dual cover crop mixtures to increase shoot biomass production and weed suppression potential

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