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Effects of nitrogen quality and quantity on weed-crop competition – a greenhouse experiment with *Avena sativa* and *Avena fatua*

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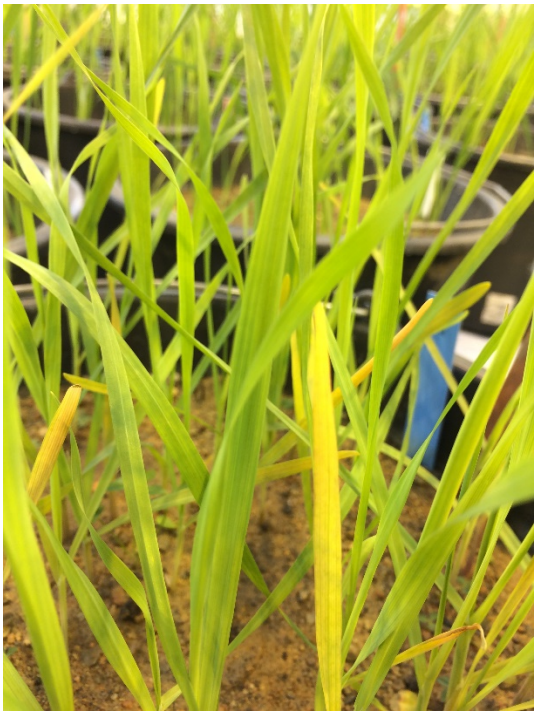

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Effects of nitrogen quality and quantity on weed-crop competition – a greenhouse experiment with *Avena sativa* and *Avena fatua*

Effekter av kvävekvalitet och kvantitet på konkurrens mellan ogräs och gröda – ett växthusexperiment med Avena sativa *och* Avena fatua

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Abstract

The intensification of agricultural activities has provided unprecedented increases in crop production. In the light of this development concerns have been raised about its negative environmental impact. High-input farm management has further reduced the weed diversity and shaped weed communities to consist of a few highly competitive weed species. Ecological theory and soil microbial processes presents another perspective focusing on managing weeds with the use of different nutrient sources and crop diversity. The establishment of distinct resource pools in soil allow nutrients to be segregated between species and reduce weed-crop competition. The aim of this study was to investigate the influence of different nutrient sources in different quantities on competitive interactions between the weed species *Avena fatua* (wild oat) and *Matricaria perforata* (scentless chamomille) and the crop *Avena sativa* (oat) intercropped with the cover crop *Trifolium resupinatum* (Persian clover). The model plants were grown in a greenhouse in pots prepared with three soil substrates containing different nitrogen sources and quantities. *A. fatua* and *A. sativa* biomass and shoot height were statistically analysed in order to investigate the species responses to changes in nitrogen quality and quantity. *A. sativa* yield loss due to *A. fatua* competition were studied at four different *A. fatua* densities. The response to changes in soil nitrogen quality, nitrogen quantity and plant density were greater for *A. sativa* compared to *A. fatua*. Higher resource pool diversity increased the interspecific competition between *A. fatua* and *A. sativa*. The unresponsiveness of *A. fatua* to changing nutrient regimes and competition suggests that reinforced competition from the crop could be used to exhaust the weed's energy reserves. Growth of *T. resupinatum* and *M. perforata* was insufficient to influence *A. sativa* in the experiment.

Key words: weed-crop competition, resource pool diversity, soil microbes, weed community

Sammanfattning

Intensifieringen av jordbrukets aktiviteter har bidragit till en produktionsökning utan motstycke. Samtidigt har en oro kring dess negativa miljöpåverkan ökat i ljuset av denna utveckling. Det moderna lantbrukets stora tillförsel av insatsvaror har lett till en minskad mångfald av ogräsarter och format ett ogrässamhälle bestående av några få starkt konkurrenskraftiga ogräs. Ekologisk teori och mikrobiella markprocesser bidrar med ett annat perspektiv med fokus på ogräskontroll, utifrån val av näringskällor och ökad mångfald av grödor i växtföljden. Genom att etablera åtskilda pooler av resurser i marken möjliggörs en uppdelning av näringen mellan arter med en minskad konkurrens mellan ogräs och gröda som följd. Målet med denna studie var att utforska vilket inflytande olika näringskällor, med varierande näringsmängd, har på konkurrensen mellan ogräsarterna *Avena fatua* (flyghavre) och *Matricaria perforata* (baldersbrå) och grödan *Avena sativa* (havre) samodlad med mellangrödan *Trifolium resupinatum* (persisk klöver). Modellväxterna odlades i växthus i krukor med tre jordsubstrat innehållande olika kvävekällor samt olika mängd kväve. Biomassa och planthöjd från *A. fatua* och *A. sativa* registrerades och analyserades i olika modeller för att utreda arternas respektive känslighet för förändrad kvalitet av kväve och kvävemängd. Skördebortfall av *A. sativa* till följd av konkurrens från *A. fatua* studerades vid fyra olika planttätheter av *A. fatua*. Responsen av förändrad kvävekvalitet och kvävemängd samt planttäthet var större för *A. sativa* i jämförelse med *A. fatua*. En större diversitet av näringskällor ökade mellanartskonkurrensen mellan *A. fatua* och *A. sativa*. *A. fatua*s okänslighet gentemot förändrade näringsbetingelser och konkurrens antyder att en förstärkt konkurrens från grödan kan användas till att uttömma ogräsets energireserver. Tillväxt av *T. resupinatum* och *M. perforata* var otillräcklig för att påverka *A. sativa* i försöket.

Nyckelord: ogräs-grödkonkurrens, diversitet av näringskällor, markmikrober, ogrässamhälle

Populärvetenskaplig sammanfattning

Konkurrensen om lättillgänglig gödsel mellan ogräs och gröda är stor. Genom att tillföra olika näringskällor och variera växtföljden kan en uppdelning av näringsresurser ske i marken. Detta i kombination med en rikare ogräsflora kan bidra till att minska ogräsens negativa påverkan på grödor.

Att endast ett fåtal ogräsarter idag påträffas i många jordbruksmarker ses som ett framsteg i kontroll av ogräs. Faktum kvarstår att de kvarvarande ogräsen har fortsatt stor negativ påverkan och begränsar livsmedelsproduktionen. En ensidig växtföljd och ett kortsiktigt perspektiv på ogräskontroll med herbicider har format ett artfattigt men konkurrenskraftigt ogrässamhälle. I motsats till detta kan en ökad artrikedom av ogräs medföra minskad konkurrens gentemot grödor. Genom att bibehålla en rik ogräsflora kombinerat med tillförsel av näring från djur- och gröngödsling samt utökad mångfald av grödor i växtföljden förutspås en minskad konkurrens från ogräs. Denna förändrade skötsel leder till en etablering av olika näringspooler som inte är direkt tillgängliga för alla växtarter. Dessa pooler kan delas upp med hjälp av mikroorganismer i marken som samarbetar med olika växtarter och förmedlar näringen till dessa. Resultatet blir att gröda och ogräs inte konkurrerar om samma resurser och en större mängd ogräs kan tolereras i fält utan sänkt skörd. Målet med denna studie var att utforska vilket inflytande olika näringskällor, med varierande näringsmängd, har på konkurrensen mellan ogräsarterna flyghavre (*Avena fatua*) och baldersbrå (*Matricaria perforata)* och grödan havre (*Avena sativa*) samodlad med mellangrödan persisk klöver (*Trifolium resupinatum*). Växterna odlades i växthus i krukor fyllda med tre olika jordtyper. Planthöjd mättes över tid och skördad biomassa vägdes för att analysera arternas känslighet mot förändrad kvalitet och mängd av kväve. I detta försök gick det inte att visa att jord med kväve från mer komplexa källor leder till minskad ogräskonkurrens. Gensvaret av förändrad tillväxt vid olika kvävekvalitet och mängd var större för havre jämfört med flyghavre. Flyghavrens okänslighet gentemot förändrade näringsbetingelser och konkurrens antyder att en förstärkt konkurrens från grödan kan utnyttjas för att uttömma ogräsets energireserver. Den persiska klövern och baldersbrån lyckades inte växa tillräckligt i experimentet för att påverka havren.

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Abbreviations

AIC_c	Akaike's information criterion, bias-corrected
BBCH	Biologische Bundesanstalt, Bundessortenamt and Chemical industry
DAS	Days after sowing
GLMM	Generalised linear mixed model
ICC	Intra-class correlation coefficients
NUE	Nutrient use efficiency
RMSE	Root mean square error
RPDH	Resource pool diversity hypothesis

1 Introduction

Intensification of agricultural land use and production has since the 1960s provided unprecedented increases in yield levels with the advent of modern agricultural techniques comprising high yielding cultivars, abundant use of mineral fertilisers, pesticides and irrigation (Foley et al., 2005). The success of what has been called the “Green Revolution” is challenged by increasing negative environmental impacts tied to modern farming methods. High-input agriculture have led to increasing greenhouse gas emissions, eutrophication of aquatic environments and reduced biodiversity above and below ground (Tilman et al., 2002). This affects the provision of ecosystem services that are the societal benefits that can be gained from ecological processes. It includes the production of natural resources and supportive services as nutrient cycling and soil formation (Tilman et al., 2002). Another major concern in high-input systems is the deterioration of soil health through erosion, nutrient leaching and loss of organic matter, all severely affecting soil biodiversity and fertility building processes (Brussaard et al., 2007; Tsiafouli et al., 2015). Regarding preservation of soil fertility, the inherent challenge lies in the feat to decrease soil disturbance and maintain soil biodiversity in intensively cultivated cropping systems, without jeopardising current yield levels.

Conservation agriculture constitutes an alternative way to sustain productivity without sacrificing above- and belowground biodiversity (Friedrich et al., 2012). It is guided by the principles of (1) reduced soil disturbance (2) permanent soil cover and (3) diverse cropping systems. However, reduced soil cultivation introduces major constraints in controlling weeds consistently, this is especially challenging to systems not using herbicides (Mirsky et al., 2012).

A small group of highly competitive weed species have gained an advantage from the management filters of undiversified crop rotations, intense soil cultivation and abundant application of herbicides (Storkey et al., 2012). The emphasis on short-term management has shaped a species poor weed flora that continues to exert a strong competitive pressure on crops, despite sustained use of herbicides (Gaba et al., 2016). A large body of knowledge exist in the field of applied weed control but

in the context of complex multi-species systems, Ward et al. (2014) perceives a need to broaden the focus of weed science and draw from wider ecological theory.

Several studies have indicated that crops in organic agricultural systems appear to be less sensitive to weed competition compared to corresponding conventional systems (Delate & Cambardella, 2004; Ryan et al., 2009; Ryan et al., 2010). Based on these finding, the resource pool diversity hypothesis (RPDH) predicts that a diversity of resources forms niches that can be segregated through partitioning and in turn decrease weed-crop competition (Smith et al., 2010). This builds upon Reynolds et al. (2003) theory of soil microbes as key agents that drive nutrient partitioning by mediation through specific plant-microbe associations. The formation of distinct resource pools is considered to be greater in agricultural systems with a more diversified selection of crops providing different compositions of plant residues in soil. Cover crops are an important contributor to the establishment of increased nutrient pool diversity as well as they are reducing the reliance on mineral fertilisers (Deguchi et al., 2007; Li et al., 2007).

Fertiliser inputs from animal and green manure influence the establishment of different resource pools where nutrients are bound in complex organic compounds requiring microbial mediation (Smith et al., 2010). Evidence in support of this model (Fig. 1) have been found in natural ecosystems that are rich in both above- and belowground biodiversity, such as forests and grasslands (Ceulemans et al., 2017; Luo et al., 2018; Phillips et al., 2013). In an agricultural context, experiments with biologically active soil inoculum from organic farms have shown to decrease weed-crop competition compared to soil from conventional farms (Johnson et al., 2017). MacLaren et al. (2018) broadened the scope of managerial options further by showing that the inclusion of sheep grazing in rotations together with crop sequence diversity influenced the number of nitrogen sources and suppressed weed abundance. The diversity of weed species was promoted and herbicide and fertiliser inputs could be decreased in the study while sustaining high crop yields.

There is lack of evidence for the applicability of RPDH in less diverse cropping systems dominated by cereals and few optional break crops. Although the RPDH predicts less interspecific competition to occur when crops and weed species differ in nutrient acquisition traits, it has not been proven whether competition between morphologically similar crops and weed species still can be affected by diverse nutrient pools (Smith et al., 2010). When weed-crop differences in nutrient root uptake are small, due to similarities in acquisition traits, it is unknown if the microbial mediation still may segregate nutrients from distinct nutrient pools.

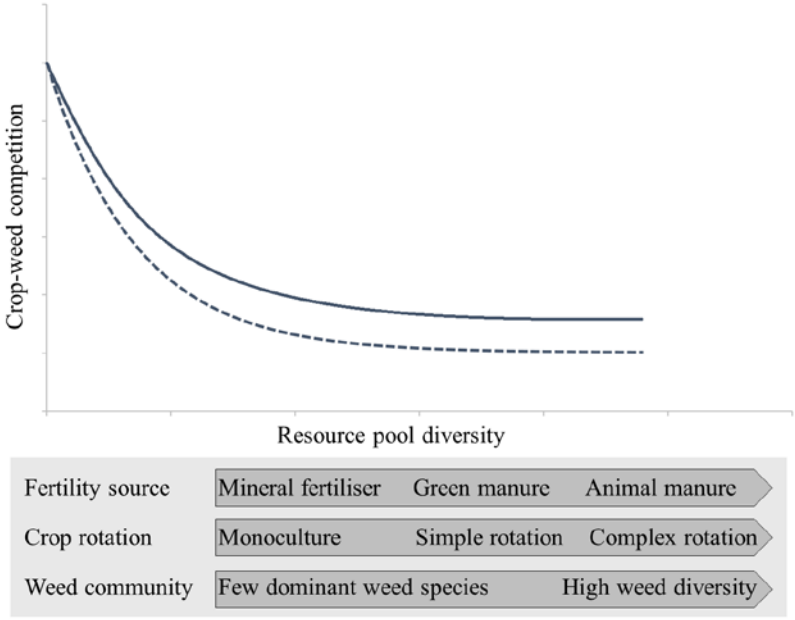

Fig. 1. Increasing resource pool diversity reduces the weed-crop competition. The resource partitioning is dependent on plants' nutrient acquisition traits. The solid line depicts the intensity of weed-crop competition between species with similar traits and the dashed line between species with different traits. The choice of fertiliser source and placement together with the choice of crop influence the establishment of resource pools as well as the weed community present in field. Figure adapted from Fig 1. & 2. in Smith et al. (2010).

1.1 Aims and hypotheses

The aim with this thesis was to (1) investigate if increased nitrogen pool diversity reduces weed-crop competition, assuming that nitrogen is the most limiting resource. The competitive effect from two weed species was studied, one with nutrient acquisition traits similar to the crop and another weed species with divergent traits. (2) Further, the response to differences in nitrogen quantity and plant density was studied between the weed species and crop. This was tested with the hypotheses:

H1 Increased nitrogen pool diversity reduces interspecific weed-crop competition due to nutrient segregation in early growth stages.

H2 The model weed species' production of biomass and competitive abilities are reduced in nitrogen limited conditions since small seeded plants are more sensitive to nutrient limitation.

H3 Increasing plant densities provoke a greater response in biomass and shoot height growth of the weed species, being more plastic compared to the crop.

Three different nitrogen sources were studied in the experiment, namely inorganic NPK fertiliser, cow manure and compost. The competitive interaction was investigated between weeds and crop in an intercropping system consisting of *Avena sativa* (oat, cv. Galant) as main crop and *Trifolium resupinatum* (Persian clover) as undersown crop. *T. resupinatum* is an annual clover and it was selected due to its high relative growth rate, early establishment and rapid covering of soil (Den Hollander et al., 2007). The model weed species in this study were *Avena fatua* (wild oat) and *Matricaria perforata* (scentless chamomille). *A. fatua* is a grass weed species similar to *A. sativa* in terms of development and nutrient acquisition traits and *M. perforata* represents a morphologically different broadleaved weed species.

2 Background

2.1 Mechanisms explaining plant diversity and coexistence

The stable coexistence of many plant species observed in a variety of ecosystems has been studied extensively and is traditionally explained by the establishment of different niches (Gause, 1934). Spatio-temporal differences in resource use carve out distinct niche spaces that prohibits a certain species from outcompeting its neighbour (Li et al., 2014). This results in a situation where intraspecific competitive interactions becomes greater than interspecific competition. The strength of niche segregation as a concept, where a diversity of species coexist over time, is self-evident in the heterotrophic animal kingdom but it has remained less apparent in plant ecology (Silvertown, 2004). The main pathways in plants for resource acquisition are very similar among most species. Few opportunities for diversification exist since all plants rely on the same resources; light, water and mineral nutrients. Nonetheless, niche segregation in plant communities are observed and can be realised through differences in traits determining drought tolerance, rooting depth and canopy development (Silvertown, 2004).

Nitrogen, is principally acquired in inorganic forms, either as reduced NH_4^+ or oxidized NO_3^-, although plants in nitrogen limited environments also acquire amino acids directly (Persson & Näsholm, 2001). In soil, nitrogen can be bound in a multitude of complex organic compounds such as proteins, chitin and nucleic acids. In order for plants to access these forms of nitrogen, microorganisms are required to degrade the organic compound and either directly mediate or release free NH_4^+ respectively NO_3^- (Reynolds et al., 2003).

Beyond niche segregation, the concept of facilitation is used to explain beneficial plant-plant interactions that allow plant coexistence and diversity by increasing available resources or suppressing other competitors and pathogens (Li, et al.,

2014). The establishment of positive plant relationships could increase nutrient acquisition in limited conditions and reduce interspecific competition. Facilitation occur either directly between plants or indirectly with plant-pollinator interactions and associations with microbes carrying out nutrient mediation by means of nitrogen fixation and mycorrhizal interaction. It has proven to be difficult to experimentally distinguish facilitation from niche segregation since both occur simultaneously in plant ecosystems, both mechanisms are therefore included in the concept of complementarity. As an example, plant association with Arbuscular mycorrhizal fungi (AMF), that supply plants with phosphorus from unavailable sources, contain both elements of niche segregation and facilitation. Some species form plant-AMF associations and occupy a distinct niche while phosphorous is simultaneously facilitated to neighboring plants (Li et al., 2014).

2.2 Weed-crop nutrient competition

A general distinction between many agricultural crops and weed species is the difference in seed size (Harbur & Owen, 2004). The smaller sized weed seeds constitute a fundamental competitive disadvantage with less seedling energy and nutrient reserves at disposal. To overcome this, many weed species have adapted to a higher relative growth rate (RGR) compared to crops, this accelerated growth is made possible by a higher uptake of nutrients early in the growing season. Nutrients, and especially nitrogen, are important resources that strongly influence weed-crop competition. Weed seedlings commonly possess longer roots than crop seedlings and this feature enables a higher nutrient use efficiency and greater accumulation of nutrients (Harbur & Owen, 2004). The high nutrient levels commonly found in agricultural fields have exerted a selection pressure towards weeds with effective nutrient acquisition traits. Harbur & Owen (2004) asserts that more attention could be directed towards nutrient management as a tool in weed control strategies and avoid the exclusive focus on fulfilling crop nutrient requirements. A study in responses to increasing nitrogen levels showed that 15 weed species accumulated more shoot biomass and 8 weed species increased in root biomass compared to wheat (Blackshaw et al., 2003). This suggests that the strategy of solely supplying high levels of readily available nitrogen could fertilise weeds more than crops and might be inadequate to increase crop competitiveness. This is not true for all combinations of crops and weeds, studies on maize and potato have demonstrated strengthened crop competition with higher nitrogen inputs (Tollenaar et al., 1994; Van Delden et al., 2002). However, it is proposed that high levels of applied nutrients primarily benefit weeds in situations where nutrients are the main limiting factor (Van Delden et al., 2002).

A higher RGR is not always an advantage in all situations, dependence on early nutrient acquisition renders weed species more sensitive to nutrient deficiencies than crops with larger seeds (Shipley & Keddy, 1988). This presents an opportunity to manage nutrient availability as a way to influence the weed abundance when other resources are non-limiting. Restrictions in nutrient availability early in the growing season can strongly influence weed-crop competition at later stages by suppressing the initial advantage of weeds' rapid growth rates (Liebman & Davis, 2000). Different fertilisation strategies have shown to affect early nutrient availability, among them are the placement of fertiliser in bands (Kirkland & Beckie, 1998), timing of fertilisation with split applications (Angonin et al., 1996) and the use of different nutrient sources such as manure, crop residues and compost (Liebman & Davis, 2000). Composted manure and crop residues from legumes show a similar effect of delayed nitrogen mineralisation since the nutrients are bound in organic material, requiring to be decomposed by microorganisms before made available (Deluca & Deluca, 1997; Varco et al., 1993).

Whether organic nutrient sources can reduce weed biomass by a slower release of available nutrients early in the season remains a debated issue. It is further important to keep in mind that nutrients from organic sources may form a foundation for complementarity and reduce interspecific competition (Smith et al., 2010). Dyck et al. (1995) demonstrated that incorporation of leguminous green manure reduced weed biomass compared to mineral fertilisation. Additionally, Davis & Liebman (2001) presented evidence that certain weed species can be selectively suppressed by application of organic manure. Contradictory to their findings, Blackshaw et al. (2005) showed in 4-year trial that composted manure had a less suppressive effect on weed biomass and weed seedbank and reduced the wheat yield when compared to banded application of mineral fertiliser. Nitrogen accumulated with yearly applications of composted manure, weed biomass increased over time since the slow release of available nitrogen was carried over to the succeeding year but no information regarding shifts in weed species composition was provided. This indicates that no segregation of nutrient pools between weeds and crop occurred in the trial, given that the composition of the weed community remained the same.

2.3 Plant-microbe nutrient mediation in soil

Soil microorganisms constitutes the vast majority of all living organisms belowground and display a diversity of functional roles (Bender et al., 2016). Bacteria and fungi together with nematodes, earthworms and arthropods are an integral part in supportive ecosystem services that can positively influence crop productivity by

regulating carbon and nutrient cycles, decomposition, soil formation and structure (Bommarco et al., 2013).

Competition for nutrients is not only restricted to interactions between plants, despite the flow of nutrients from soil via microorganisms to plants there is a strong initial competition for nutrients, particularly in the rhizosphere (Kuzyakov & Xu, 2013). There are temporal differences in nutrient acquisition between microorganisms and plants that follows the pattern of rapid utilisation of excessive carbon by microorganisms from root exudates. Microorganisms initially immobilise nutrients but the fast growth rate eventually leads to a depletion of carbon that starves the microorganisms around the roots. A flush of previously unavailable nutrients is then released and made accessible to plant root uptake. Thus, limited nutrient availability around the root stimulates the production of carbon compounds in the rhizosphere that in time yields available nutrients from dead microbial biomass. In search for available carbon substrates, microorganisms venture out of the rhizosphere to mine organic matter which in turn releases organically bound nutrients, constituting an influx of nutrients that can further feed the system. Key to this process are saprotrophic fungi that contribute to soil formation and fertility by degrading soil organic material and mineralise organically bound nutrients (Kuzyakov & Xu, 2013.

At the center of the nitrogen cycle, diazotrophs are found fixating atmospheric N_2 into plant available NH_4^+, either by Rhizobia in symbiotic association with leguminous plants or by non-associative free-living species such as *Azospirillum* (Kennedy et al., 1997). Plant availability and leaching of nitrogen is further regulated by soil microbes carrying out processes of nitrification and denitrification (Bender et al., 2016). Arbuscular mycorrhiza fungi (AMF) species can, apart from scavenge for and mediate phosphorous, intercept excessive flows of nutrients and reduce N_2O emissions derived from denitrification (Cavagnaro et al. 2015). Plant interactions with AMF are somewhat unspecific since a wide range of plant species successfully form associations with the fungi. It is more importantly the variation of the plants' responses that differentiates the outcome and forms the basis for interspecific plant complementarity and facilitation (Eom et al., 2000).

These outlined soil biology processes, often overlooked in cultivated systems, collectively play a significant role in the productivity of plant ecosystems. Interference from land-use management commonly bypass and decrease the reliance on nutrient services, exchanging them with application of mineral fertilisers which increases the dependence on external fossil energy sources (Vitousek et al., 1997). Decreases in soil biodiversity, with lower abundance of functional groups, has been observed in regions across Europe with increasing land-use intensification (Tsiafouli et al., 2015). It has been argued that many functional groups may be redundant and that species richness as a measurement is less indicative of ecosystem functionality (Hunt & Wall 2002; Nielsen et al., 2011). Loss of soil biodiversity can

be compensated by other groups without altering the overall functionality of ecosystems, instead the community composition serves as stronger indicator for the function of soil processes. Wagg et al. (2014) has shown that organic decomposition and mediation of nutrients to aboveground biomass decline only when certain key groups such as mycorrhizal fungi or nematodes disappear. Ecosystem multifunctionality is to a certain extent positively correlated to high soil biodiversity and that the sensitivity to changes in function increases in simplified soil communities. This a condition usually met in intensively cultivated agricultural systems (Tsiafouli et al., 2015). A distinction can be made between the function of organic decomposition, that remain less sensitive to changes in soil community composition and narrow functions of mycorrhizal association, denitrification and nitrification that are more dependent on specific community composition (Schimel & Schaeffer, 2012). Soil organic carbon constitutes a key driver for soil microbial communities and a critical threshold for loss of ecosystem function has been suggested to exist in soils containing less than 2% soil organic carbon (Loveland & Webb, 2003).

2.4 Cover crops and intercropping

Cover crops are plants maintained as living ground cover that can be integrated in a cropping system either by cultivation between growing seasons or mixed with the main crop in an intercropping system (Hartwig & Ammon, 2002). The inclusion of cover crops offers substantial ecosystem services in agricultural systems with their capacity to reduce soil erosion and nutrient leaching as well as increasing soil organic matter. They further constitute an integral part in increasing the nutrient pool diversity by forming an additional source of organic nutrients that can be segregated between weed and crop (Deguchi et al., 2007; Li et al., 2007). Leguminous cover crops form associations with nitrogen-fixing Rhizobia-bacteria, constituting a source of organic nitrogen available to the succeeding crop when decomposed. (Hartwig & Ammon, 2002). Intercropping systems with leguminous species are known to overyield due to a more efficient use of nitrogen (Szumigalski & van Acker 2006). Although fixated nitrogen from symbiotic Rhizobia association is immobilised and restricted during the growth period to leguminous species, it indirectly reduces the competition for NO_3^- in soil. This results in increased nitrogen availability for other non-leguminous species, known as the sparing effect (Szumigalski & van Acker 2006). A study in intercropping with phosphorus limited conditions indicated that overyielding can be further explained by increased phosphorus availability (Li et al., 2007). The observed increase in phosphorus availability for the main crop was explained by interspecific interactions in the rhizosphere, leading

to the conclusion that phosphorus was directly facilitated and not partitioned due to differences in nutrient acquisition (Li et al., 2007).

Cover crops can influence the weed abundance negatively by occupying the same niche space as the weed community and replace weed species (Médiène et al., 2011). Germination of weed seeds can be suppressed by desiccated cover crops that intercept light and release inhibitory exudates of allelopathic compounds (Phatak, 1992). Competition from living and established cover crops can suppress the weed biomass through light, water and nutrient competition (Den Hollander et al., 2007). However, leguminous cover crops receive their nitrogen needs from Rhizobia symbiosis and do not compete for this nutrient with weeds. The lack of selective competition by cover crops against specific plant species remains an inherent trade-off. Just as a cover crop may compete well against weed populations it can exert an equally strong negative effect on the harvested main crop, causing yield losses when grown simultaneously. A crucial aspect to this is the timing of emergence where the cover crop needs to be established in time to compete against early emerging weeds (Buhler et al., 2001). To avoid unwanted competition, the peak growth of the cover crop should be managed to not coincide with the time when the main crop is sensitive to competition (Bergkvist, 2003; Médiène et al., 2011). The significance of cover crops in weed competition is inconclusive and to some extent related to growing conditions. Weed-cover crop competition is mainly determined by the biomass production ability of the cover crop and hence limited by the climatic conditions. Hartwig & Ammon (2002) reported that undersowing competitive clover species in corn can provide sufficient weed control, comparable to herbicide treatments. When growing and incorporating cover crops between crop seasons red clover showed a similar weed suppressive effect while oilseed radish and cereal rye increased weed biomass (Hill et al., 2016).

2.5 Weed flora and diversity

The choice of including two model weed species in this study, one morphologically resembling the crop (*A. fatua*) and one different from the crop (*M. perforata*) is motivated by the tenet of increased weed diversity as a prerequisite for niche segregation (Smith et al., 2010). From a simplistic agronomical point of view, the drastic decline in weed species diversity seen over the last 50 years may appear as a feat of success in limiting the number of weed species present in field (Storkey & Neve, 2018).

Still, the remaining weed species in field are often highly competitive and continue to limit crop yields. They have adapted to dominating crop rotations by retaining traits that are tolerant to control measures in short rotations and efficient at acquiring abundant nutrient resources (Gaba et al., 2016). Contrary to this, findings imply that high weed species richness is uncorrelated to more abundant weed biomass and may potentially reduce the overall weed-crop competition in field. This is corroborated by studies showing that an increased diversity of weed species may either reduce crop yield losses (Storkey & Neve, 2018) or have no negative effect on crop performance (Pollnac et al., 2009).

A weed community with species that possess a variety of functional traits occupy segregated niches that allow a spatio-temporal partitioning of resources (Silvertown, 2004). This functional differentiation, conceptualised as the complementarity effect, acts as a stabilising factor against the establishment of dominant species that in isolation might become strong crop competitors (Hooper et al., 2005). In such a diverse system, interspecific competition for the same resources diminishes. However, it requires an environment that contains elements for niche segregation, such as different resource pools that are mediated separately to specific species (Smith et al., 2010). The diversity of a weed community can further be used as an indicator of the stability of the agricultural system and its breadth of niches (Fig. 1) (Storkey & Neve, 2018). It indirectly reveals the management history and the selection pressure from herbicide and fertilisation use, crop rotation and soil cultivation practices. Weed species diversity is consequently both affecting the competitive pressure in field and remains an emergent response to the management of the system (Hooper et al., 2005).

3 Materials and method

3.1 Experimental design

This experiment was conducted in a greenhouse at Ultuna, Swedish University of Agricultural Sciences. Loamy sand with <0.5% organic carbon and 5 kg N ha^{-1} (0.13 mg NO_3-N $100g^{-1}$ dry substance) was used as base substrate for mixing three soil substrates with different diversities of nutrient sources (Table 1). The three nitrogen substrates used in the experiment were inorganic NPK fertiliser (YaraMila PROMAGNA, 4.4% NO_3-N, 6.6% NH_4-N, 4.6% P and 17.6% K), cow manure containing 4.9 kg N ton^{-1} and compost containing 9.11 kg N ton^{-1} (Table 1).

The target amount of total nitrogen in all soil substrates was 50 kg ha^{-1}, with the base substrate included. This constitutes 50% of recommended nitrogen application in spring cereals (Jordbruksverket, 2019) and is motivated by a moderate nutrient restriction necessary to study the effects of nutrient competition in a limited growth period. Substrate A was mixed with 45 kg N ha^{-1} inorganic fertiliser (YaraMila PROMAGNA), substrate B with 20 kg N ha^{-1} cow manure and 25 kg N ha^{-1} inorganic fertiliser and substrate C with 20 kg N ha^{-1} cow manure and 25 kg N ha^{-1} compost (Table 2). Due to experimental error in the compost nitrogen analysis, soil substrate C was mixed with an insufficient amount of compost and ended up with half of the intended nitrogen content (Table 1). The aim with the soil substrates were changed to compare soil substrates A and B in regard to difference in nitrogen quality and A and C to compare the difference in nitrogen quantity. Although a difference in quality still existed between A and C it was assumed that the quantitative difference would have a stronger effect, obscuring the differences in quality. The inorganic fertilizer pellets were ground before incorporated in the top 2 cm soil layer to avoid an uneven distribution. Added amounts of nitrogen were calculated from pot surface area and no additional fertiliser was applied during the growth period. The measurements of the pots used in the experiment were 9 L, 27 cm in diameter

and 18 cm in height. Each pot contained 14 kg of the prepared soil substrates and were placed in the greenhouse to settle during a week. Samples of each mixed soil substrate were collected and total nitrogen content analysed. 3 replicates for all soil substrate were prepared. The pots were placed in a completely randomised design, covering the whole greenhouse. A temperature gradient existed in one direction with lower temperatures close to windows situated along one side of the greenhouse, this was accounted for by measuring the individual pot distances to the windows. The photoperiod in the greenhouse was set to 12 h light at 200 μE m^2 s^1 and the day/night temperature was 25°C/10°C. The total amount of pots in the experiment were 162. 3 soil substrates * 2 weed species (*A. fatua* and *M. perforata*) * 9 densities * 3 replicates = 162.

Table 1. *Nitrogen balance from analysis of mixed soil substrates A, B and C. Nitrogen forms measured per 100 g dry weight (DW). A-B was compared in regard to nitrogen quality and A-C in regard to nitrogen quantity.*

Soil substrate	NO_3-N (mg $100g^{-1}$ DW)	NH_4-N (mg $100g^{-1}$ DW)	N-min (kg ha^{-1})
A (NPK)	0.78	0.53	111.0
B (NPK, cow manure)	0.70	0.47	99.4
C (Cow manure, compost)	0.56	0.08	54.5

Table 2. *Nitrogen content analysis of organic fertilisers added to soil substrates B and C. Nitrogen content measured from dry substance (DS).*

Substrate	DS (%)	N-min (kg t^{-1} DS)	NH4-N (kg t^{-1} DS)
Cow manure	26.0	4.90	1.6
Compost	38.5	9.11	0.6

Germination rate was derived from pre-germinating 100 seeds of each species in trays filled with soil base substrate. The trays were put in the greenhouse and watered daily. Germinated seeds were counted and divided by 100. All pots were seeded with 28 seeds of *A. sativa*, the target density was 20 plants per pot. *A. sativa* seeds were sown in two rows with 12 cm row spacing at a depth of 3 cm. *T. resupinatum* was seeded together with one weed species, either *A. fatua* or *M. perforata*, in a response model design with totally 9 plant density combinations (Fig. 2, left). The target plant densities for cover crop and weeds, both separate and mixed, were 150, 300, 600 plants m^{-2}. When unmixed, *T. resupinatum* was sown with 11, 21 and 42 seeds, *A. fatua* with 18, 34 and 68 seeds and *M. perforata* with 32, 58 and 116 seeds per pot. Both cover crop and weed seeds were placed randomly in the pots. *A. fatua* was sown at a depth of 3 cm, the smaller seeds of *T. resupinatum* and *M. perforata* were sown at 0,5 cm. 0,5 kg of soil was added on top after sowing and the pots were watered daily with tap water. One week after sowing, *A. sativa* was

thinned to 20 plants per pot and the remaining species to their respective target densities. When studying the effect of increasing *A. fatua* plant densities against the fixed density of *A. sativa*, an additive experimental design was used (Fig. 2, right).

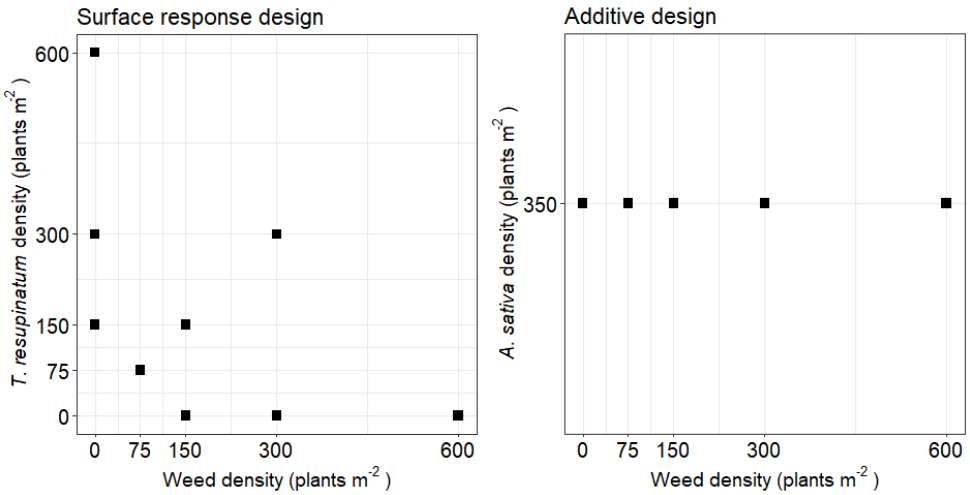

Fig. 2. Experimental designs used in this study. Surface response model (left) takes intra- and interspecific plant-plant competition into account, the cover crop (*Trifolium resupinatum*) and weed species (*Avena fatua* and *Matricaria perforata*) were grown mixed and unmixed. The additive design (right) were used to study the competitive effect from weed species by increasing densities of a competitor against the target species (*Avena sativa*).

3.2 Measurements

Non-destructive measurements were made at a weekly interval during a period of five weeks after emergence (Table 3). Five plants were sampled randomly from each pot for the measurements. Development stage was assessed for all species according to the BBCH scale (Meier, 1997). Shoot height was measured for *A. sativa* and *A. fatua* to determine the growth rate over time.

Measurement of chlorophyll content in the youngest developed leaves was made with a SPAD meter, measuring the index of relative chlorophyll content between -9.9 to 199.9, as an indicator for nitrogen accumulation in *A. sativa* and *A. fatua*.

Above- and belowground biomass of the four plant species was harvested 42 days after sowing (DAS) (Table 3). Shoots and roots were separated for all species except *A. sativa* and *A. fatua* since their roots grew into each other and became inseparable. The biomass was then dried at 80°C for 48h before weighing.

Table 3. *Measurements made of the model plants* Avena sativa, Trifolium resupinatum, Avena fatua *and* Matricaria perforata *in the greenhouse experiment at specific days after sowing (DAS). Non-destructive measurements of shoot height (mm), development stage (BBCH) and chlorophyll content (SPAD) were done during growth period. The biomass dry weight (g) was weighed after harvest.*

Species	Parameters	Measurements (DAS)
***A. fatua* treatment**		
A. sativa	Shoot and root biomass (g DW)	42-43
	Shoot height (mm)	8, 15, 22, 29, 35, 42
	BBCH	8, 15, 22, 29, 35, 42
	Chlorophyll content (SPAD)	35, 42
T. resupinatum	Shoot and root biomass (g DW)	42-43
	BBCH	8, 15, 22, 29, 36, 42
A. fatua	Shoot biomass (g DW)	42-43
	Shoot height (mm)	15, 22, 29, 35, 42
	BBCH	15, 22, 29, 35, 42
	Chlorophyll content (SPAD)	35
***M. perforata* treatment**		
A. sativa	Shoot and root biomass (g DW)	41-42
	Shoot height (mm)	8, 15, 22, 28, 36, 41
	BBCH	8, 15, 22, 28, 36, 41
	Chlorophyll content (SPAD)	36, 41
T. resupinatum	Shoot and root biomass (g DW)	41-42
	BBCH	8, 15, 22, 29, 36, 41
M. perforata	Shoot and root biomass (g DW)	41-42
	BBCH	15, 22, 29, 36, 41

3.3 Data analysis

3.3.1 Surface response interaction analysis

A generalised linear mixed model (GLMM) using the *glmer* function in R (Bolker et al., 2009) was used to analyse the effect of (1) *T. resupinatum* density on *A. sativa* and *A. fatua* root and shoot biomass and (2) *M. perforata* density on *A. sativa* root and shoot biomass.

The model included soil substrate and weed or cover crop plant density as fixed factors and pot distance to windows as well as replicate numbers as random factors. Interactions between the fixed factors were analysed with a one-way analysis of variance test (Anova). Least square means of *A. sativa* shoot biomass (g) were calculated for each fixed factor level. Marginal R^2 was calculated for each model, a

value that estimates the amount of variation that is explained by fixed factors (Nakagawa & Schielzeth, 2013). Further, intra-class correlation coefficients (ICC) were determined, representing the amount of variation explained by random factors in hierarchical data (Nakagawa et al., 2017).

3.3.2 Nitrogen quality and quantity analysis

The effect of soil nitrogen quality and quantity on *A. sativa* root and shoot biomass with and without *A. fatua* competition was analysed with GLMMs using soil substrates as fixed factor. The effect was also studied on *A. fatua* shoot biomass. Pair-wise comparison of soil substrate A and B was made for nitrogen quality analysis and soil substrate A and C for nitrogen quantity analysis.

A. sativa and *A. fatua* shoot nutrient use efficiency (NUE) per pot was calculated accordingly:

$$Shoot\ NUE\ (g/Nmin\ kg\ ha^{-1}) = (B/N) \quad (1)$$

where *B* is the shoot biomass (g) and *N* the N-min (kg ha^{-1}) content of the respective soil substrates. The shoot NUE was then analysed with a GLMM using soil substrate as fixed factor. Pot distance to windows, replicate numbers and *T. resupinatum* density were included as random factors. The output of the GLMMs was analysed according to the procedure in surface response interaction analysis.

3.3.3 Rectangular hyperbola model, additive design

The following analyses considered the *A. fatua* treatment as an additive design with increasing *A. fatua* densities against a fixed *A. sativa* density (Fig. 2, right). The tested hypotheses were *H1* and *H2*.

Harvested *A. sativa* shoot biomass (g) from each pot was converted into yield loss (%) caused by *A. fatua* competition that was calculated separately for each soil substrate:

$$YL\ (\%) = \left(\frac{M - B}{M}\right) * 100 \quad (2)$$

where *M* is the mean of *A. sativa* shoot biomass (g) per pot, derived from all pots without *A. fatua* competition. *B* denotes the mean of *A. sativa* shoot biomass (g) from individual pots in competition with *A. fatua*. These calculations were made separately for each soil substrate in order to make them comparable since *M* for each soil substrate differed. The calculated yield loss was plotted in relation to *A. fatua*

density which indicated that a rectangular hyperbola function could be fitted to the data (Cousens, 1985):

$$YL = \left(\frac{I * x}{1 + \left(\frac{I}{A}\right) * x} \right) * 100 \quad (3)$$

where *I* describes the yield loss increase (%) per unit of weed plant density, *x*, at the point where weed density approaches 0. *A* describe the yield loss increase (%) per unit of weed plant density at the point where weed density approaches ∞. The rectangular hyperbola model was fitted with the *nls* function in R to estimate *I* and *A* values corresponding to the yield loss data (Oliveira et al., 2018). One full model and three reduced models were produced (Table 4) and then compared using Akaike's information criterion, bias-corrected for smaller sample sizes (AIC_c; Equation 4), to test statistically significant differences for *I* and *A* between the soil substrates (Hurvich & Tsai, 1991).

Table 4. *Full and reduced rectangular hyperbola models with estimated parameters explaining* A. sativa *shoot biomass yield loss (%) at low weed densities (*I*) and high densities (*A*) for soil substrates A, B and C.*

Rectangular hyperbola model	Estimated parameters
Full model	*I* and *A* for each soil
Reduced 1	One *I* and *A* for all soils
Reduced 2	One *I* for all soils, *A* for each soil
Reduced 3	*I* for each soil, one *A* for all soils

$$AIC_c = -2\log(l) + 2K * (\frac{n}{n - K - 1}) \quad (4)$$

l is the likelihood function, *K* the number of estimated parameters (*A. fatua* density and soil substrate) and *n* the sample size. The best model is the one with the lowest AIC_c value, according to the criterion, and this was analysed with the *AICmodavg* package in R.

Goodness-of-fit was used to test the accuracy of the models by calculating the root mean squared error (RMSE):

$$RMSE = \sqrt{\frac{RSS}{n - p - 1}} \quad (5)$$

where *RSS* is the residual sums of squares, *n* the number of data points and *p* the number of model parameters (Mayer & Butler, 1993). Another rectangular hyperbola model was constructed with *A. fatua* shoot biomass as fixed factor according to aforementioned procedure.

3.3.4 Three parameter logistic growth model

A. sativa and *A. fatua* shoot height development was studied over time to investigate the effect of increasing plant density as well as soil nitrogen quality and quantity between the species. A three parameter logistic growth model was constructed with the *drm* function in R (Ritz & Streibig, 2005) to study the *A. sativa* and *A. fatua* shoot height dynamics over time:

$$f\big(z,(b,d,e)\big) = \frac{d}{1+\exp\{b(\log(z)-\log(e))\}} \tag{6}$$

where *z* represents days after sowing (DAS) and parameter *e* the number of days to reach 50% of final *A. sativa* shoot height (mm) at harvest date 42 DAS. Parameter *b* represent the slope around *e* and *d* the maximum *A. sativa* shoot height (mm). One logistic curve of *A. sativa* shoot height with parameters b, d and e was fitted for each of the five *A. fatua* densities to determine the competitive effect on *A. sativa* height development.

In order to compare the *b* slopes between different *A. fatua* densities, the *A. sativa* height was normalised accordingly:

$$log\left(\frac{d-y}{y}\right) = b(\log(z)-\log(e)) \tag{7}$$

where *d* represents the maximum shoot height and *y* the measured shoot height at respective points in time. The normalised shoot height attained a value between 0-1. Another three parameter logistic model was fitted using the normalised shoot height where the final height at 42 DAS was fixed to 1 in order to make the *b* parameter comparable between different *A. fatua* densities and soil substrates.

Final *A. sativa* shoot height derived from the unnormalised model was analysed with a GLMM using soil substrate and *A. fatua* density as fixed factors. Pot distance to windows as well as replicate numbers were included as random factors.

4 Results

4.1 *T. resupinatum* and *M. perforata* interaction

The competitive effect of *T. resupinatum* and *M. perforata* at four densities was studied on *A. sativa* root and shoot biomass production. *T. resupinatum* competition towards *A. fatua* shoot biomass was further investigated to determine its effect on the weed.

There was no evidence of any competitive effect from both *T. resupinatum* and *M. perforata* at densities 75, 150, 300 and 600 plants m^{-2} on *A. sativa* shoot or root biomass production (Fig. 3). There was a significant difference between *A. sativa* root and shoot biomass production at the *M. perforata* density of 75 plants m^{-2} (Fig. 3b), indicating that the allocation of assimilate to shoots were greater at this particular density. The same effect can be observed at *T. resupinatum* density of 75 plants m^{-2} (Fig. 3a), however, differences in shoot and root biomass did not occur at any other *M. perforata* or *T. resupinatum* density. Low R^2 values in both analyses indicate that the fixed factors *T. resupinatum* and *M. perforata* density explained very little variation in *A. sativa* shoot biomass. The random factors Window distance and Replicate numbers explained little variation as well in the *M. perforata* analysis (Appendix, Table 2) and no variation at all in *T. resupinatum* analysis (Appendix, Table 1).

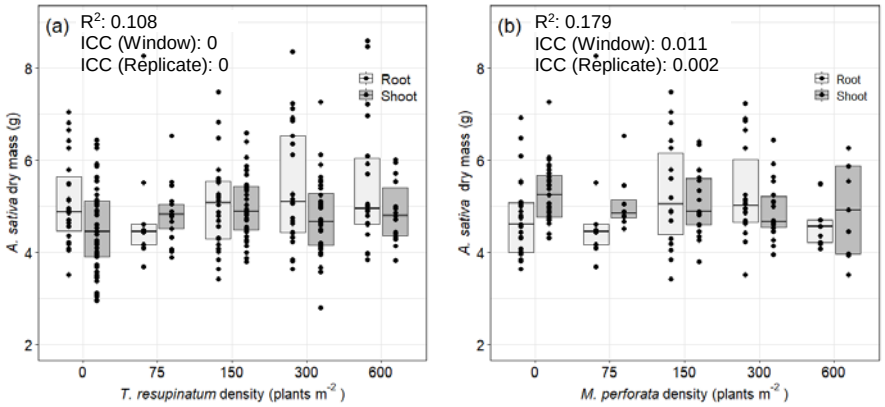

Fig. 3. Effect of (a) *Trifolium resupinatum* density (plants m^{-2}) on *Avena sativa* shoot and root biomass (g) production at 42 days after sowing (DAS). Effect of (b) *Matricaria perforata* density (plants m^{-2}) on *A. sativa* shoot and root biomass (g) production at 42 DAS. The lower and upper hinges correspond to the first and third quartiles and the line inside the boxes represent the median. ICC corresponds to intra-class correlation coefficients of the random effects Window distance and Replicate.

T. resupinatum density had no effect on *A. fatua* shoot biomass when both species were mixed at densities 150 and 300 plants m^{-2} (Fig. 4) The random factors window distance and replicate numbers explained no variation in *A. fatua* shoot biomass analysis (Appendix, Table 3), consequently, the plant density of *T. resupinatum* was excluded as a fixed factor in the following analyses with *A. fatua* and *A. sativa*.

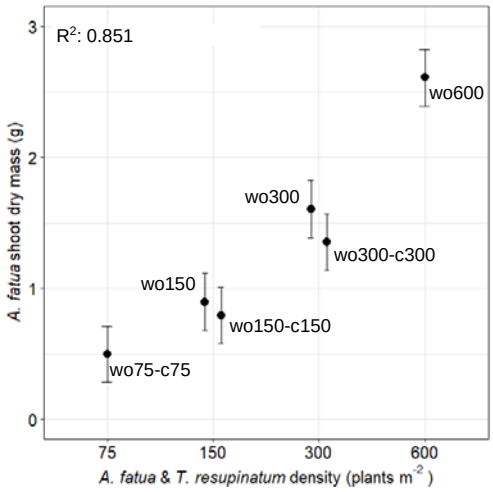

Fig. 4. Effect of *Trifolium resupinatum* density (plants m^{-2}) on *Avena fatua* shoot biomass (g) production at 42 days after sowing. Mean shoot biomass (g) in pots with *T. resupinatum* (c) and *A. fatua* (wo). Error bars signifies the standard deviation of the least square means.

The germination of *M. perforata* was uneven and most pots did not reach the target densities. The first *M. perforata* seedlings started to emerge 4-6 days after *A. sativa* and *T. resupinatum* but the overall *M. perforata* emergence was protracted and extended to weeks after this. *A. sativa* can be considered to be the sole crop in the *M. perforata* treatment, uninfluenced by both *M. perforata* and *T. resupinatum* that were treated as random factors in the consequent analyses.

4.2 Influence of soil nitrogen quality and quantity on *A. sativa* and *A. fatua* biomass

Effects on *A. sativa* and *A. fatua* biomass growth due to differences in soil nitrogen quality was investigated between soil substrate A and B. Effects from differences in soil nitrogen quantity were studied between soil substrate A and C. Soil A and B contained similar amounts of NO_3-N and NH_4-N (mg 100g-1 DW) (Table 1), A was selected to represent the higher nitrogen fraction in all subsequent quantity analyses. *A. sativa* and *A. fatua* nutrient use efficiency (NUE) was studied to investigate if soil quality or quantity as well as *A. fatua* density had an effect on the species biomass accumulation and shoot allocation.

4.2.1 Nitrogen quality

The response due to changes in soil quality was greater for *A. sativa* compared with *A. fatua*. *A. sativa*, when competing with *A. fatua*, responded with higher shoot biomass production in soil substrate A compared to B (Fig. 5; Appendix, Table 4). *A. sativa* shoot biomass in A and B was inverted when *A. fatua* increased in plant density, but no statistically significant interaction between soil substrates and *A. fatua* density was found (Appendix, Table 4). The fixed factors explained the variation to some extent (R^2: 0.403) as well as the random factors Window distance (ICC: 0.4048) and Replicate number (ICC: 0.1478). There was no interaction between Window distance and Replicate (Appendix, Table 4). *T. resupinatum* density as random factor explained no variation.

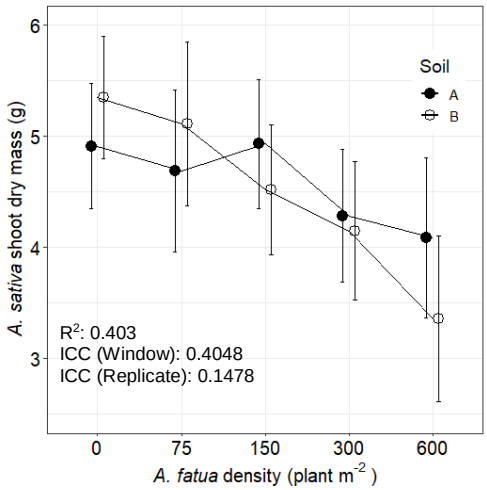

Fig. 5. A trend of higher *Avena sativa* shoot biomass (g) with increasing *Avena fatua* density (plants m^{-2}) in soil substrate A (NPK, N-min = 111.0 kg ha^{-1}) compared to B (cow manure and NPK, N-min = 99.4 kg ha^{-1}) at 42 days after sowing. Error bars signify the standard deviation of the least square means. ICC corresponds to intra-class correlation coefficients of the random effects Window distance and Replicate.

A. sativa shoot biomass production in monoculture was not affected by the qualitative differences between soil substrate A and B (Appendix Fig. 1; Table 5). Further, the chlorophyll content in *A. sativa* shoots was not affected by the soil quality when competing with *A. fatua* (Appendix, Fig. 2; Table 6). Higher nitrogen pool diversity present in soil B did not increase shoot biomass production, shoot height or chlorophyll content in *A. sativa*.

A. fatua shoot biomass was not affected by the qualitative differences between soil A and B (Appendix Fig. 3; Table 7).

4.2.2 Nitrogen quantity

A. sativa shoot and root biomass production in monoculture increased with higher nitrogen levels present in soil A compared to soil C (Fig. 6). There was a significant difference in both root and shoot biomass between soil A and C (Appendix, Table 8, 9) but the low R^2 values in both analyses show that very little of the variation could be explained by the soil substrates as fixed factor (Fig. 6). Window distance as random factor explained more variation (ICC: 0.1554) in the shoot analysis (Fig. 6a).

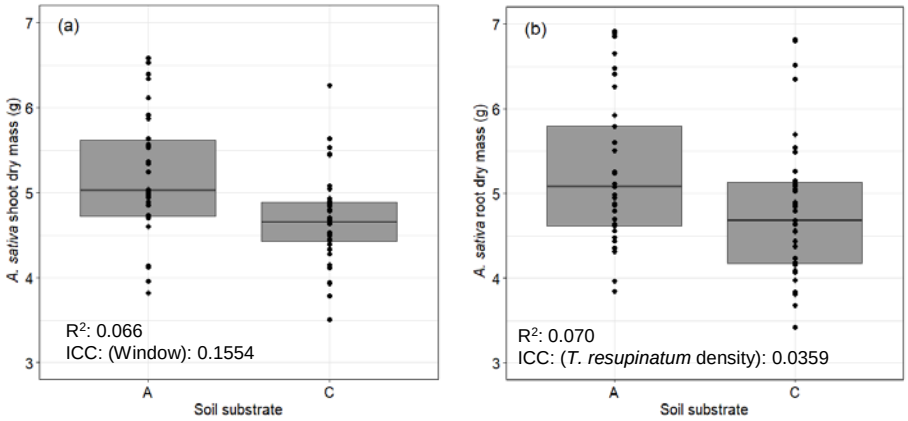

Fig. 6. Avena sativa (a) shoot and (b) root biomass (g) increased with higher nitrogen quantity in soil substrate A (NPK, N-min = 111.0 kg ha^{-1}) compared to C (cow manure and compost, N-min = 54.5 kg ha^{-1}) at 42 days after sowing. The lower and upper hinges correspond to the first and third quartiles and the line inside the boxes correspond to the median. ICC corresponds to intra-class correlation coefficients of the random effects Window distance and *Trifolium resupinatum* density.

A. sativa shoot biomass production in competition with *A. fatua* was higher in soil A compared to C across all *A. fatua* plant densities (Fig. 7; Appendix Table 10). Most of the variation was explained by the fixed factors (R^2: 0.491) although all random factors had some influence (Fig. 7).

A. fatua shoot biomass was not affected by differences in nitrogen quantity (Appendix, Fig. 4; Table 11). The response to changes in soil quantity was greater for *A. sativa* compared with *A. fatua*.

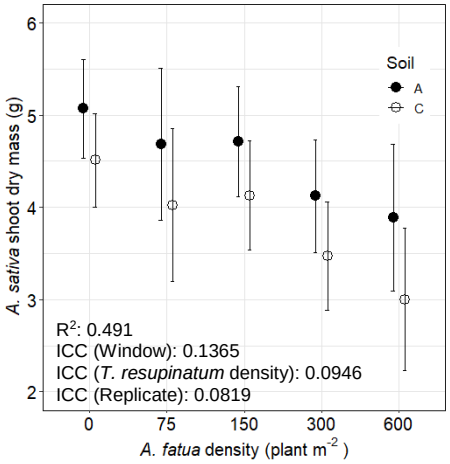

Fig. 7. A trend of higher *Avena sativa* shoot biomass (g) in soil substrate A (NPK, N-min = 111.0 kg ha^{-1}) compared to C (cow manure and compost, N-min = 54.5 kg ha^{-1}) across all *Avena fatua* densities (plants m^{-2}) at 42 days after sowing. Error bars signify the standard deviation of the least square means. ICC corresponds to intra-class correlation coefficients of the random effects Window distance, *Trifolium resupinatum* density and Replicate.

4.2.3 Nutrient use efficiency

A. sativa shoot NUE was higher in the nitrogen limited soil substrate C compared to A (Fig. 8a; Appendix, Table 12). A high R^2 (0.725) indicated that the variation in *A. sativa* shoot NUE was well explained by the soil substrates as fixed factors (Fig. 8a). *A. fatua* shoot NUE showed a tendency to increase in nitrogen limited soil substrate C compared to A (Fig. 8b; Appendix, Table 12). There was a statistically significant difference between the soil substrates ($p < 0.001$) but the variation of *A. fatua* shoot NUE was not sufficiently explained by soil substrates as fixed factor (R^2: 0.110). The random factor *T. resupinatum* density had greater influence on the variation (ICC: 0.4018). The comparison of soil substrate A and C contains elements of both quantitative and qualitative differences but the difference in nitrogen content can is assumed to be of a greater influence than the quality. This further underline that *A. sativa* is more responsive to changes in nitrogen quantity compared with *A. fatua*.

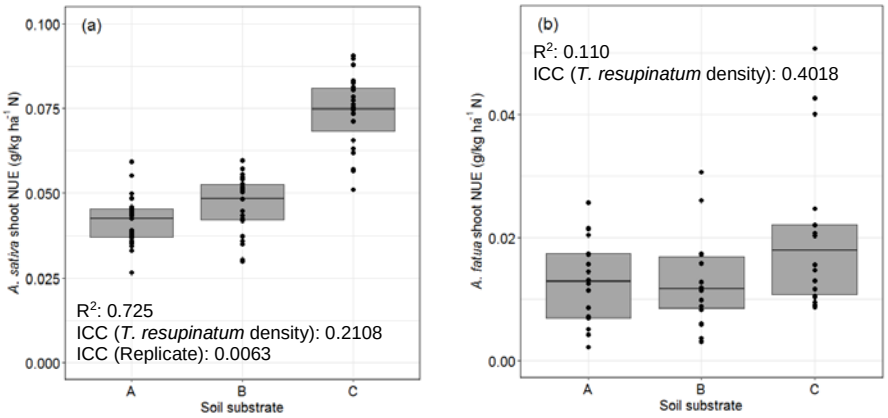

Fig. 8. (a) *Avena sativa* shoot nutrient use efficiency (g kg^{-1} ha^{-1} N; NUE) responded to changes in nitrogen quantity at 42 days after sowing (DAS). (b) *Avena fatua* shoot NUE (g kg^{-1} ha^{-1} N) was unaffected by soil nitrogen quality and quantity at 42 DAS. Soil substrate C (cow manure and compost, N-min = 54.5 kg ha^{-1}) compared with A (NPK, N-min = 111.0 kg ha^{-1}) and B (cow manure and NPK, N-min = 99.4 kg ha^{-1}). The lower and upper hinges correspond to the first and third quartiles and the line inside the boxes correspond to the median. ICC corresponds to intra-class correlation coefficients of the random effects *Trifolium resupinatum* density and Replicate.

4.3 *A. sativa* yield loss by *A. fatua*

The competitive ability of *A. fatua* against *A. sativa* was studied with an additive experimental design where *A. fatua* density increased towards a fixed *A. sativa* density. The effect of nitrogen quality on *A. sativa* shoot yield loss (%) from *A. fatua* competition was studied between soil substrate A and B and the effect nitrogen quantity was studied between soil substrate A and C. The yield loss of *A. sativa*

shoot biomass was analysed with two rectangular hyperbola models, one using *A. fatua* density and the other *A. fatua* shoot biomass as fixed factors. In the models, the *I* parameter represents the yield loss (%) per unit of increasing *A. fatua* density or shoot biomass at the point where these factors approach 0. This yield loss adheres to situations where the weed starts to appear in field. The *A* parameter represents the yield loss (%) per unit of increasing *A. fatua* density or shoot biomass at the point where *A. fatua* density approaches ∞. This yield loss applies to situations where the weed is dominating at high densities in field.

When comparing the full and reduced rectangular hyperbola models the reduced model 3, with separate *I* values for each soil and one *A* value for all soils, resulted in the lowest AIC_c value for both *A. fatua* density and shoot biomass (Table 5). This indicated that there was a significant difference between soil substrates for parameter *I* but not *A*. The goodness-of-fit test with Root mean square error (RMSE) followed the same trend, the reduced model 3 had the lowest value and was the most accurate model to explain *A. sativa* shoot yield loss (Table 5). In reduced model 3 model, four parameters were estimated, three *I* parameters for each soil substrate and one *A* for all soil substrates.

Table 5. *Selection of rectangular hyperbola models explaining* Avena sativa *shoot biomass yield loss (%) due to* Avena fatua *density (plants* m^{-2}*) and shoot biomass (g) based on biased-corrected Akaike's information criterion (*AIC_c*) and root mean square error (RMSE). Parameter* I *correspond to* A. sativa *yield loss (%) at low* A. fatua *densities and parameter* A *at high* A. fatua *densities.*

		***A. fatua* density**		***A. fatua* shoot biomass**	
Model	Parameters	AIC_c	RMSE	AIC_c	RMSE
Full model	*I* and *A* for each soil	613.24	1.178	613.07	
Reduced 1	One *I* and *A* for all soils	609.16	1.186	404.14	1.443
Reduced 2	One *I* for all soils *A* for each soil	609.11	1.167	400.79	1.363
Reduced 3	*I* for each soil, one *A* for all soils	608.73	1.164	399.75	1.350

The yield loss of *A. sativa* shoot biomass increased with higher *A. fatua* plant densities and *A. fatua* shoot biomass (Fig. 9). At low *A. fatua* densities and shoot biomass (*I*), *A. sativa* shoot yield loss (%) was higher in soil B with higher nitrogen pool diversity compared to soil A, according to estimates from the reduced 3 rectangular hyperbola model (Fig. 9; Table 6). When comparing nitrogen quantity at low *A. fatua* densities and shoot biomass (*I*), *A. sativa* shoot yield loss (%) was higher in soil C with lower nitrogen content compared to soil A (Fig. 9; Table 6). At high *A. fatua* densities and shoot biomass (*A*) neither nitrogen quality or quantity

affected *A. sativa* shoot yield loss (%), the estimated *A* parameter was the same for all soil substrates (Table 6).

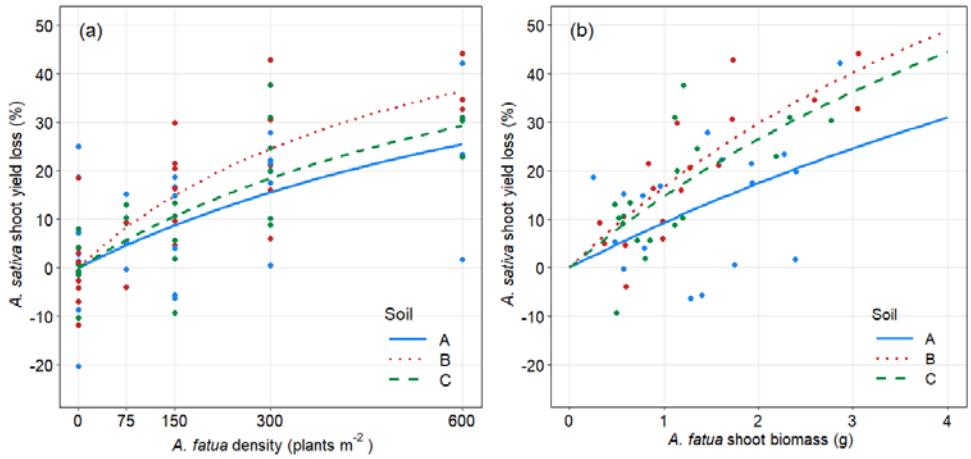

Fig. 9. Increasing (a) *Avena fatua* density (plant m^{-2}) and (b) *A. fatua* shoot biomass (g) caused a higher *Avena sativa* shoot biomass yield loss (%) at 42 days after sowing. Soil substrate B (cow manure and NPK) showed the highest yield loss when *A. fatua* density and shoot biomass increased with one unit from 0 (*I*). No differences between soils were found when *A. fatua* density and shoot biomass approached infinity (*A*).

Table 6. *Differences in* Avena sativa *yield loss (%) between soil substrates at low* Avena fatua *densities (plants* m^{-2}*) and shoot biomass (g) at 42 days after sowing (DAS), denoted with parameter* I. *No difference in A. sativa yield loss (%) between soil substrates at high* A. fatua *densities (plants* m^{-2}*) and shoot biomass (g) at 42 DAS, denoted with parameter* A. *Parameter* I *and* A *estimated with reduced 3 rectangular hyperbola model.*

Parameters	Soil substrate	Estimate (%)	Standard error	t-value	p-value
***Avena fatua* density**					
I	A	0.066	0.019	3.543	<0.001 ***
	B	0.125	0.042	3.011	0.004 **
	C	0.083	0.024	3.489	<0.001 ***
A	ABC	70.534	32.530	2.168	0.033 *
***Avena fatua* shoot biomass**					
I	A	9.988	2.302	4.339	<0.001 ***
	B	19.023	5.356	3.552	<0.001 **
	C	16.465	3.981	4.136	<0.001 ***
A	ABC	136.34	123.12	1.107	0.274

4.4 *A. sativa* shoot height growth development

A. sativa and *A. fatua* shoot height development was studied over time to investigate the effect of increasing plant density as well as soil nitrogen quality and quantity between the species. *A. sativa* and *A. fatua* shoot height, measured at specific points in time, was fitted with a three parameter logistic model producing parameters *b*, *d* and *e* for each soil substrate and *A. fatua* density.

The final shoot height of *A. sativa* was suppressed at higher *A. fatua* densities in all soil substrates (Fig. 10; Appendix, Table 14, 15, 16). This was not significant in soil substrate C but the same trend can be observed (Fig. 10c; Appendix, Table 16). The slope (parameter *b*) of *A. sativa* shoot height at 50% of maximum height, showed a tendency to increase at higher *A. fatua* densities (Table 7). *A. fatua* shoot height had a steeper slope compared with *A. sativa* but showed a tendency to decrease at higher *A. fatua* densities (Table 7). The response in shoot height growth was greater for *A. sativa* compared to *A. fatua*.

Table 7. *The slope of* Avena sativa *and* Avena fatua *shoot height at 50% maximum shoot height (mm/day) with different soil substrates and* A. fatua *densities (plants* m^{-2}*) at 42 days after sowing. Parameter* b *is derived from the three parameter logistic model with normalised shoot height (height (mm)/d) forced to 1.*

Soil	*A. fatua* density (plant m^{-2})	*A. sativa, b* (mm/day)	*A. fatua, b* (*mm/day*)
A	0	-2.28	
	75	-2.45	-3.80
	150	-2.46	-4.87
	300	-2.54	-4.56
	600	-2.90	-3.76
B	0	-2.34	
	75	-2.25	-4.61
	150	-2.43	-3.66
	300	-2.30	-3.46
	600	-2.62	-3.73
C	0	-2.61	
	75	-2.72	-3.19
	150	-2.59	-3.28
	300	-2.58	-3.73
	600	-2.86	-2.71

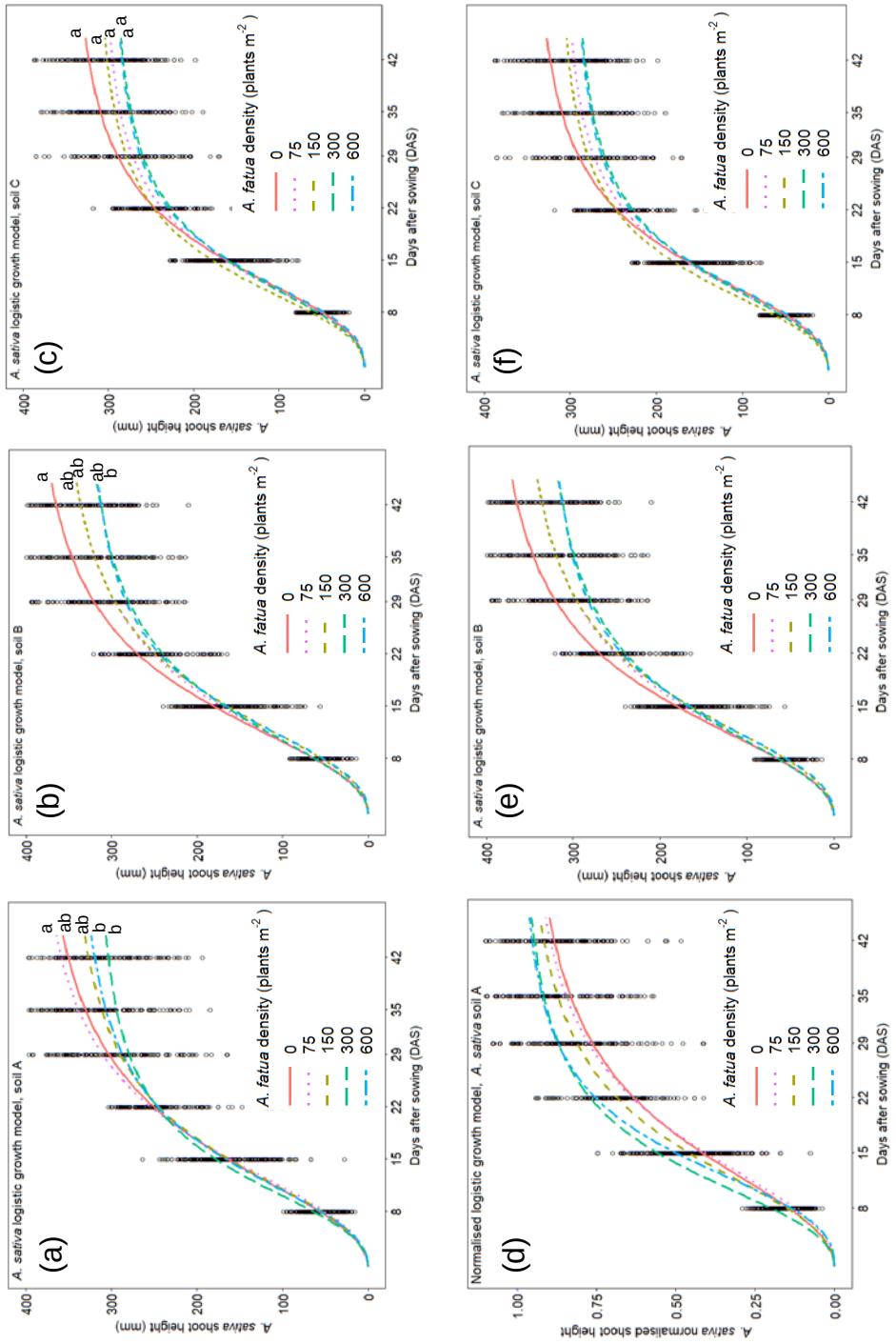

Fig. 10. (a, b & c) Three parameter model with actual *Avena sativa* shoot height (mm) at different *Avena fatua* densities (plants m^{-2}) at 42 days after sowing (DAS). Final *A. sativa* shoot height (mm) was lower when *A. fatua* density (plants m^{-2}) increased in (a) soil A and (b) soil B but not in (c) soil C. Lettering denotes significant difference in final shoot height between treatments derived from GLMM. (d, e & f) Three parameter model with normalised *A. sativa* shoot height at different *A. fatua* densities (plants m^{-2}) at 42 DAS, final height fixed to 1.

Competition from *A. fatua* had a negative effect on the development of *A. sativa* shoots (Fig. 11; Appendix, Table 17). *A. sativa* development stage (BBCH) was lower at *A. fatua* density 600 (plant m^{-2}) at DAS 29, 35 and 42 compared with lower densities. The fixed factors *A. fatua* density and DAS explained the variation strongly (R^2: 0.953). This indicates that competitive effects on development starts to appear four weeks after sowing.

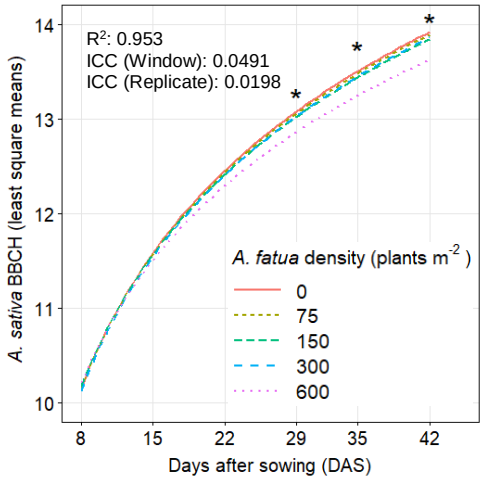

Fig. 11. Avena sativa development stage (BBCH) was affected by the highest *Avena fatua* density (600 plant m^{-2}) at 29, 35 and 42 days after sowing (DAS). The plotted curves for each *A. fatua* density (plants m^{-2}) are derived from least square means of integer BBCH-values. Asterisks denote significant difference in p-value between *A. fatua* density at specific DAS. ICC corresponds to intra-class correlation coefficients of the random effects Window distance and Replicate.

The chlorophyll content in the youngest developed leaves of *A. sativa*, measured at DAS 42, showed a tendency to decrease with higher *A. fatua* density (Fig. 12; Appendix, Table 18). However, very little variation in chlorophyll content was explained by *A. fatua* density (R^2: 0.060), the random factor Window distance (ICC: 0.117) influenced the variation to a greater extent. *A. sativa* chlorophyll content was not affected by the different soil substrates (Appendix, Table 18).

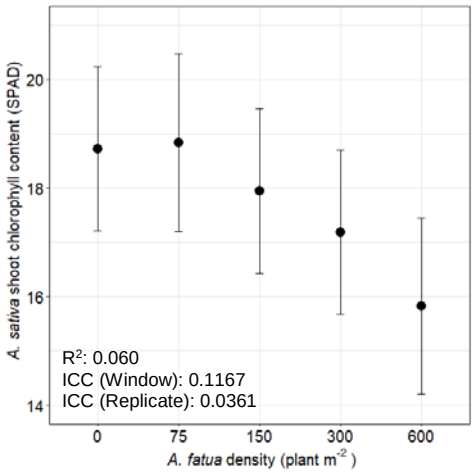

Fig. 12. A trend towards decreasing *Avena sativa* shoot chlorophyll content (SPAD) with higher *Avena fatua* density (plants m^{-2}) at 42 days after sowing. Error bars signify the standard deviation of the least square means. ICC corresponds to intra-class correlation coefficients of the random effects Window distance and Replicate.

5 Discussion

5.1 Resource pool diversity

The approach to eliminate and control weed species as means to reduce their competition against crops has over the past decades prompted concerns about its economic and environmental effects (Gaba et al., 2016). In response, this has generated calls to better integrate ecological theory governing weed-crop interactions within weed management (Ward et al., 2014). The resource pool diversity hypothesis (RPDH) constitutes a framework to understand how farm management and cropping rotations, through the establishment of nutrient pools in soil, can influence and reduce weed-crop competition without extensive use of external agricultural inputs (Smith et al., 2010).

In this study, differences in nitrogen pool diversity was studied in a mechanistic approach with two weed species in a cereal and clover intercropping system. *A. sativa* shoot yield loss (%) increased with higher nitrogen pool diversity at low *A. fatua* densities, when fitted to a rectangular hyperbola model (Fig. 9). No reduced *A. fatua* competition with higher nitrogen pool diversity was found in additional analyses with *A. sativa* shoot biomass production (Appendix, Fig. 1), chlorophyll content (Appendix, Fig. 2) and shoot height development (Fig. 10; Table 7). The hypothesis that increased nitrogen pool diversity reduces interspecific weed-crop competition between *A. sativa* and *A. fatua* (*H1*) was rejected. An extended growth period with prolonged nutrient acquisition by roots could reveal a more pronounced effect from differences in nitrogen quality.

It was assumed that nitrogen represented the most limiting resource in this experiment. Considering that nitrogen was the only analysed nutrient it is possible that other nutrients were in fact more limiting. The uncertainty of other nutrients limiting growth was higher in the more complex and undefined nutrient sources of cow manure and compost compared to the inorganic fertiliser where all mineral nutrients

were defined. Another possible limiting resource is water. The pots were watered daily and no water was observed to run through the pots but the soil dried up fast at some occasions, the day temperature in the greenhouse reached up to 25°C. The water holding capacity of the soil can be considered low since it contained >50% sand, however, the addition of cow manure and compost increases the soil water holding capacity. It cannot be ruled out that water at some points was more limiting than nutrients, overriding any effect of differences in nutrient pools. The water deficiency could be assumed to follow the temperature gradient and, thus, had a greater limiting effect on the plants' growth in pots at a distance from the windows.

Mineralised nitrogen content in soil substrates A and B was considered equal (Table 1) and no mediation of plant unavailable nitrogen can be said to have occurred. If organically bound nitrogen would be mediated to plants by microbes in soil substrate B, the biomass production should be expected to increase. This was not observed, instead *A. sativa* shoot biomass yield loss from *A. fatua* competition increased in soil substrate B (Fig 9). A possible explanation for this could be the different spatial profile of nitrogen between soil substrate A and B. In soil substrate B, the cow manure was mixed in the whole pot while all nutrients in soil substrate A resided in the top 2 cm layer. A greater allocation of biomass to roots to access deeper buried nitrogen could have occurred in soil substrate B. This was not investigated since *A. sativa* and *A. fatua* roots were inseparable. Further, soil microbial immobilisation of nutrients in soil substrate B could have occurred at a greater extent since the addition of cow manure increased the C:N ratio.

5.2 *A. sativa* and *A. fatua* response to nitrogen quality and quantity

The observed crop and weed responses to differences in nitrogen quality and quantity, nutrient use efficiency (NUE) and plant-plant competition suggests that *A. sativa* is more adaptive to changes in the environment than *A. fatua*. *A. sativa* shoot biomass was negatively affected by higher nitrogen pool diversity (Fig. 5) and lower nitrogen content when competing with *A. fatua* (Fig. 7). Further, *A. sativa* NUE increased with lower nitrogen content (Fig 8a). The trend in responses to nitrogen quality and quantity were followed for *A. sativa* shoot biomass yield loss modelled with a rectangular hyperbola (Fig. 9).

In the three parameter logistic model, the slope of parameter *b*, explaining the rate of *A. sativa* shoot height growth at 50% of maximum height, increased as a response to higher *A. fatua* competition (Fig. 10). In contrast, *A. fatua* shoot biomass was unaffected by nitrogen quality (Appendix, Fig. 2) and quantity (Appendix, Fig.

4) at different plant densities in all above-mentioned analyses. The two tested hypotheses could both be rejected:

H2 The model weed species' production of biomass and competitive abilities are reduced in nitrogen limited conditions since small seeded plants are more sensitive to nutrient limitation.

H3 Increasing plant densities provoke a greater response in biomass and shoot height growth of the weed species, being more plastic compared to *A. sativa*.

Consequently, the strategy of *A. fatua* appears to be directed towards retaining a robust growth pattern regardless of changes in nutrient regime and plant density. The competitive effect from *A. sativa* on *A. fatua* was not studied, the experimental design could only take intraspecific *A. fatua* competition into account. This result suggest that *A. sativa* is more plastic than *A. fatua* during early growth stages which contradicts prior studies, describing *A. fatua* as responsive to differences in applied nitrogen (Balyan & Malik, 1989) and having a higher NUE than *Triticum aestivum* (wheat) (Kirkland & Beckie, 1998). However, Morishita & Thill (1988) found that *A. fatua* was less efficient at utilising nitrogen compared to *Hordeum vulgare* (barley).

When calculating the shoot NUE in this study, a bundle of traits was merged. It indirectly involved nutrient acquisition by roots, allocation of nitrogen to shoots and soil nitrogen content. Which of these processes that dominated could not be distinguished. The calculated NUE might only reflect the allocation of nitrogen to shoots and not the amount of nitrogen uptake by roots. Therefore, it is not possible to assert with confidence that no response at all occurred in *A. fatua* at different nitrogen quantities. The smaller seeded *A. fatua* showed a more rapid shoot height growth rate (Table 7, *b* slope), compared to *A. sativa*. However, the expected sensitivity to sub-optimal nutrient levels, observed by Shipley & Keddy (1988), could not be shown in this experiment (Appendix, Fig. 4). *A. fatua* has been found to develop a larger rooting system compared to *T. aestivum* with a greater ability to utilise and compete for nutrients (Haynes et al., 1991). In this experiment there could exist differences in root development but the lack of data on segregated roots made this impossible to study.

In order to reduce crop yield loss from *A. fatua* in field, the findings in this study supports a strategy of exploiting the weed's unresponsiveness by increasing crop competition. This could include management practices of growing competitive tall-stature cultivars and increasing seed rates, complemented with a diverse cropping rotation with less spring cereals, as suggested by Harker et al. (2009). It should be noted that higher cultivars have a lower potential yield compared to modern semi-

dwarf cultivars, due to differences in carbon and nitrogen partitioning to stem instead of grain (Sinclair, 1998). However, in conditions with high weed pressure, in low input systems without the option of herbicides, this is a compromise that could be acceptable. Increased seed-rates may only be relevant in extensive systems with low initial seed rates, the *A. sativa* density of 350 plants m^{-2} in this experiment should not be exceeded. Higher plant densities introduce the risks of lodging and higher disease incidence, it also increases the costs of seeds and sowing operations (Lemerle, 2004). The improvement of crop competition could additionally be facilitated by traits controlling early vigour that do not necessarily affect the potential yield (Bertholdsson, 2005).

5.3 *T. resupinatum* and *M. perforata* growth

Since *T. resupinatum* showed no competitive effect towards either *A. sativa* (Fig. 3a) or *A. fatua* (Fig. 4), there was no possibility to test any hypotheses regarding cover crop competition. The low biomass production of *T. resupinatum* was likely caused by unfavourable soil properties of the base soil substrate. Root nodulation of *T. resupinatum* was not studied quantitatively but the presence of nodules on some roots could be observed during harvest. Very few nodules were red and active. *T. resupinatum* plant density explained a lot of variation in the analysis of shoot NUE (Fig. 8). The low nitrogen level in soil substrate C had less effect on *T. resupinatum* growth that allowed it to have a greater influence on *A. sativa* and *A. fatua* growth. A lower sensitivity to nitrogen deficiency is expected from the leguminous *T. resupinatum*, being able to fix its own nitrogen. When analysing measurements of *A. sativa* shoot height (Appendix, Table 14, 15 & 16), there is a possibility of unestimated random effects from *T. resupinatum*. Shoot height of *T. resupinatum* was not measured and therefore it could not be included as random factor. The random effect of pot distance to windows explained significant variation across all analyses but the growth of *T. resupinatum* and *M. perforata* was equally restricted at all placements in the greenhouse.

The late emergence of *M. perforata* constituted a disadvantage towards competition against *A. sativa*. It has been reported that winter annual *M. perforata*, not starting from seed, reduces spring cereal yields up to 10 times more than summer annual *M. perforata* (Douglas et al., 1991). Consequently, simultaneous sowing of *M. perforata* and *A. sativa* is not optimal to study the competitive effect from *M. perforata*. Water stress could further be a factor that influenced both *T. resupinatum* and *M. perforata* growth. *M. perforata* is described as a species performing best in cool and moist conditions (Douglas et al., 1991).

5.4 Future research

The concept of resource pool diversity carries a great potential if it can be experimentally shown that diversified management influences and reduce weed-crop competition in field. This will amount to a transformational shift in how agricultural weeds are viewed. It would profoundly change the idea of weeds as something that in all situations should be eliminated, instead it could be approached as a component in the system that is managed and to some extent tolerated, without reducing crop yields. Active propagation of more weed species in field could be needed where a species rich weed flora has been lost. This is, to some extent already adopted with cover and subsidiary crops, a non-harvested plant species that is sown, managed and tolerated in field (Médiène et al., 2011). In this experiment, the performance of the model plants varied and the nitrogen content between soil substrates was uneven. This leaves several questions regarding weed diversity, nutrient pool diversity and the effect from cover crops to be answered in future experiments.

To investigate the competitive effect from a weed species or a cover crop with different growth patterns compared to the crop, the seeds should be sown and established prior to the crop. The weed species and cover crop need to accumulate enough biomass in order to have an effect on the crop in a limited growth period. To rule out uncertainties regarding *T. resupinatum* nodulation, future experiments should be inoculated with *Rhizobia trifolii*. In an experiment with a well-established cover crop, the following hypotheses could be tested:

i. The cover crop show weed suppressive abilities in regard to biomass accumulation.
ii. There is a critical point where weed abundance suppresses cover crop growth.
iii. Intercropped main crop and cover crop compete synergistically against the weed species for acquisition of nutrients, water and light.
iv. There is a proportional relationship between the biomass of main crop and cover crop, the main crop yield decreases with increasing cover crop biomass.

Regarding the (iii) synergistic competition, it could be investigated if the crop and cover crop have complementary competitive traits, that when mixed exert a greater negative impact on weed abundance than their individual competition added together. These traits could include canopy and root architecture as well as time of emergence.

To ensure that distinct nutrient pools are established, soils could be collected from fields with (1) undiversified nutrient inputs and cropping rotations, representing low resource pool diversity and (2) diversified management with high resource pool diversity. Another possibility is to use soils with different management history as inoculum in pots with a soil base substrate to ensure that the microbial flora from different sites are represented (Johnson et al., 2017). The use of soil from agricultural fields increases the likelihood that microorganisms needed for nutrient mediation are present. Any nutrient imbalance between the soils could be equalised with additional nutrient application. It would also be beneficial to analyse other nutrients than solely nitrogen, such as phosphorous and potassium, to elucidate which nutrient that is the most limiting. Separation of roots between *Avena* species in pots can be achieved by fitting a nylon mesh as a barrier, allowing root exudates to pass through but omitting intermingling of roots (Li et al., 2007).

Water as limiting resource should be avoided by making sure that the pots are watered at daily intervals. Further, the selected soils should preferably have a higher water holding capacity compared to the soil in this experiment with >50% sand. Efforts to keep the day temperature around 20 °C could also be made.

Within the field of soil microbiology, there is a need for studying plant-microbe interactions in more detail. The different mechanisms governing nutrient segregation could be further investigated to deduce their relative importance. Species with large and extensive root systems could be grown with and without soil microbes known to mediate nutrients, this could indicate the contribution from microbial mediation. The specificity of plant-microbe associations is also relevant to study with a weed species and crop that are morphologically similar in order to determine the potential of nutrient segregation between the species.

The spatio-temporal aspect of plant nutrient acquisition from nutrient pools could be approached by studying root architecture of crop and weed. Relevant traits to study are root length, root elongation rate and number of root tips, all known to influence nutrient competitive abilities (Stevanato, 2011). In this manner, the nutrient competition derived from overlapping growth patterns in time and space could be explored.

6 Conclusion

This thesis comprised a greenhouse experiment with the aim to investigate the influence of nitrogen pool diversity on weed-crop competition with a mechanistic approach. The competitive effect from the grass weed species *A. fatua*, morphologically similar to the crop *A. sativa*, was studied when grown in three soil substrates with different nitrogen quality and quantity. Further, the respective weed and crop responses to differences in nitrogen quality and quantity as well as plant density were studied. *A. sativa* response in biomass accumulation and shoot growth was greater with changes in soil nitrogen quality, quantity and plant density compared to *A. fatua*. A higher nitrogen pool diversity did not decrease the interspecific competition between *A. fatua* and *A. sativa*. Limitations in soil nitrogen content increased interspecific weed-crop competition between *A. fatua* and *A. sativa*.

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Appendix

Table 1. *Analysis of variance (Anova) on GLMM with response variable* A. sativa *biomass and fixed factors* T. resupinatum *density and Biomass type.*

Response variable: *A. sativa* biomass				
Fixed factors:	$\chi 2$	Df	p-value	
T. resupinatum density	7.864	4	0.097	
Biomass type (Root & shoot)	14.271	1	<0.001	***
T. resupinatum density:Biomass type	7.081	4	0.132	
Random effects:	Variance	Standard deviation		
Window	0.000	0.000		
Replicate	0.000	0.000		
Residual	2.121	1.456		
Number of observations: 268		Groups: Window, 42; Replicate, 3		

Table 2. *Analysis of variance (Anova) on GLMM with response variable* A. sativa *biomass and fixed factors* M. perforata *density and Biomass type.*

Response variable: *A. sativa* biomass			
Fixed factors:	$\chi 2$	Df	p-value
M. perforata density	5.016	4	0.286
Biomass type (Root & shoot)	0.203	1	0.652
M. perforata density:Biomass type	7.839	4	0.098
Random effects:	Variance	Standard deviation	
Window	0.037	0.193	
Replicate	0.006	0.077	
Residual	0.838	0.915	
Number of observations: 162		Groups: Window, 38; Replicate, 3	

Table 3. *Analysis of variance (Anova) on GLMM with response variable* A. fatua *shoot biomass and fixed factors* T. resupinatum *and* A. fatua *density.*

Response variable: *A. fatua* shoot biomass				
Fixed factors:	$\chi 2$	Df	p-value	
T. resupinatum density	216.78	3	<0.001	***
A. fatua density	141.33	2	<0.001	***
T. resupinatum density: *A. fatua* density		0		
Random effects:	Variance	Standard deviation		
Window	0.000	0.000		
Replicate	0.000	0.000		
Residual	0.094	0.307		
Number of observations: 54		Groups: Window, 31; Replicate, 3		

Table 4. *Analysis of variance (Anova) on GLMM with response variable A. sativa shoot biomass and fixed factors Soil substrate AB and A. fatua density.*

Response variable: *A. sativa* shoot biomass				
Fixed factors:	χ2	Df	p-value	
Soil substrates AB	5.008	1	0.953	
A. fatua density	37.24	4	0.000	***
Soil substrates AB:*A. fatua* density	8.956	4	0.062	.
Random effects:	Variance	Standard deviation		p-value
Window	1.644	0.406		0.065
Replicate	0.060	0.245		0.018 *
Replicate:Window				0.999
Residual	0.182	0.426		
Number of observations: 53			Groups: Window, 31; Replicate 3	

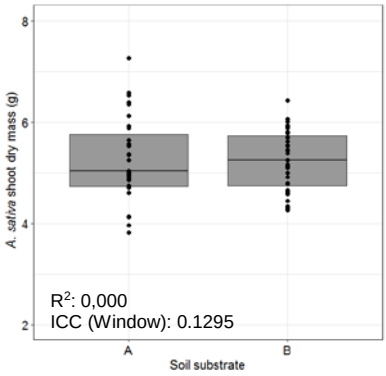

Table 5. *Analysis of variance (Anova) on GLMM with response variable A. sativa shoot biomass in monoculture with fixed factor soil substrate AB.*

Response variable: *A. sativa* shoot biomass			
Fixed factors:	χ2	Df	p-value
Soil substrate AB	0.0488	1	0.8252
Random effects:	Variance	Standard deviation	
Window	0.1090	0.3302	
Residual	0.7328	0.8560	
Number of observations: 107	Group: Window, 37		

Fig. 1. A. sativa shoot biomass production was not affected by different soil nitrogen quality in monoculture (right). Soil A (NPK, N-min = 111,0 kg ha^{-1}) compared to soil B (cow manure and NPK, N-min = 99.4 kg ha^{-1}). The lower and upper hinges correspond to the first and third quartiles and the line inside the boxes correspond to the median.

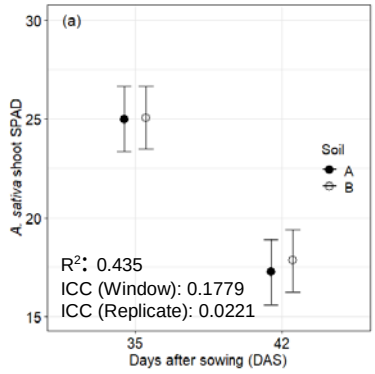

Table 6. *Analysis of variance (Anova) on GLMM with response variable* A. sativa *shoot SPAD with fixed factors soil substrate AB and Days after sowing (DAS).*

Response variable: *A. sativa* shoot SPAD				
Fixed factors:	χ2	Df	p-value	
Soil substrate AB	0.2961	1	0.5863	
DAS	338.235	1	0.00000	***
Soil substrate AB:DAS	0.4220	1	0.5159	
Random effects:	Variance	Standard deviation		
Window	3.2475	1.8021		
Replicate	0.4042	0.6358		
Residual	14.6021	3.8213		
Number of observations: 355	Group: Window, 24; Replicate, 3			

Fig. 2. A. sativa shoot chlorophyll content (SPAD) was not affected by different soil nitrogen quality when competing with *A. fatua* (left) or in monoculture (right). Soil A (NPK, N-min = 111,0 kg ha^{-1}) compared to soil B (cow manure and NPK, N-min = 99.4 kg ha^{-1}). Error bars signify the standard deviation of the least square means.

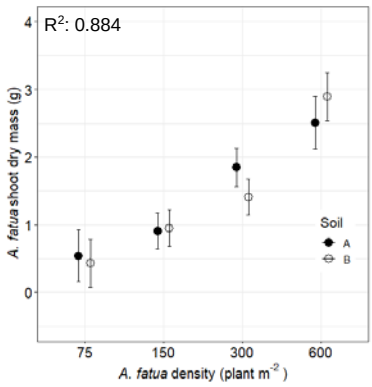

Table 7. Analysis of variance (Anova) on GLMM with response variable A. fatua *shoot biomass with fixed factors soil substrate AB and* A. fatua *density.*

Response variable: *A. fatua* shoot biomass				
Fixed factors:	χ2	Df	p-value	
Soil substrate AB	0.7067	1	0.40055	
A. fatua density	204.2862	3	0.00000	***
Soil substrate AB:*A. fatua* density	8.3622	3	0.03909	*
Random effects:	Variance	Standard deviation		
Window	0.00000	0.0000		
Residual	0.09046	0.3008		
Number of observations: 36	Group: Window, 24			

Fig. 3. A. fatua shoot biomass production was not affected by different soil nitrogen quality at different A. fatua densities. Soil A (NPK, N-min = 111,0 kg ha^{-1}) compared to soil B (cow manure and NPK, N-min = 99.4 kg ha^{-1}). Error bars signify the standard deviation of the least square means.

Table 8. *Analysis of variance (Anova) on GLMM with response variable* A. sativa *shoot biomass in monoculture and fixed factor Soil substrate AC.*

Response variable: *A. sativa* shoot biomass				
Fixed factors:	χ2	Df	p-value	
Soil substrate AC	5.008	1	0.025	*
Random effects:	Variance	Standard deviation		
Window	0.117	0.342		
Residual	0.635	0.797		
Number of observations: 72			Groups: Window, 36	

Table 9. *Analysis of variance (Anova) on GLMM with response variable* A. sativa *root biomass in monoculture and fixed factor Soil substrate AC.*

Response variable: *A. sativa* root biomass				
Fixed factors:	χ2	Df	p-value	
Soil substrate AC	5.510	1	0.019	*
Random effects:	Variance	Standard deviation		
T. resupinatum density	0.063	0.251		
Residual	1.691	1.300		
Number of observations: 72			Groups: *T. resupinatum* density, 5	

Table 10. Analysis of variance (Anova) on GLMM with response variable A. sativa *shoot biomass and fixed factors Soil substrate AC and* A. fatua *density*

Response variable: *A. sativa* shoot biomass				
Fixed factors:	$\chi 2$	Df	p-value	
Soil substrates AC	19.84	1	<0.001	***
A. fatua density	32.35	4	<0.001	***
Soil substrates AC:*A. fatua* density	0.468	4	0.977	
Random effects:	Variance	Standard deviation		
Window	0.047	0.216		
T. resupinatum density	0.032	0.180		
Replicate	0.028	0.167		
Residual	0.234	0.484		
Number of observations: 54	Groups: Window, 28; *T. resupinatum* density, 5; Replicate, 3			

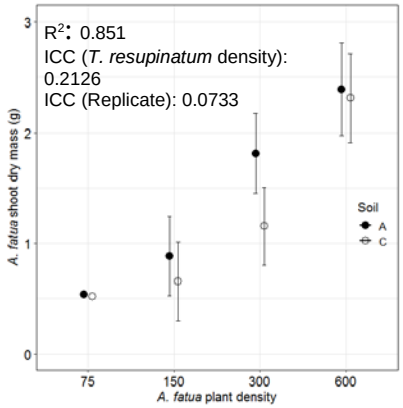

Fig. 4. A. fatua shoot biomass was not affected by different nitrogen quantities at different *A. fatua* densities (plant m^{-2}). Soil A (NPK, N-min = 111,0 kg ha^{-1}) and soil C (cow manure and compost, N-min = 54,5 kg ha^{-1}). Error bars signify the standard deviation of the least square means.

Table 11. *Analysis of variance (Anova) on GLMM with response variable* A. fatua *shoot biomass and fixed factors* A. fatua *density and Soil substrate AC.*

Response variable: *A. fatua* biomass				
Fixed factor:	$\chi 2$	Df	p-value	
A. fatua density	171.097	1	<0.001	***
Soil substrate AC	16.200	3	<0.001	***
A. fatua density: Soil substrate AC	10.861	3	0.0125	*
Random effects:	Variance	Standard deviation		
T. resupinatum density	0.0162	0.1274		
Replicate	0.0056	0.0748		
Residual	0.0545	0.2335		
Number of observations: 36	Groups: *T. resupinatum* density, 4; Replicate, 3			

Table 12. *Analysis of variance (Anova) on GLMM with response variable* A. sativa *shoot NUE and fixed factor Soil substrate ABC.*

Response variable: *A. sativa* shoot biomass				
Fixed factors:	$\chi 2$	Df	p-value	
Soil substrates ABC	265.99	2	<0.001	***
Random effects:	Variance	Standard deviation		
T. resupinatum density	0.000	0.004		
Replicate	0.000	0.001		
Residual	0.000	0.008		
Number of observations: 80	Groups: *T. resupinatum* density, 5; Replicate, 3			

Table 13. *Analysis of variance (Anova) on GLMM with response variable* A. fatua *shoot NUE and fixed factor Soil substrate ABC.*

Response variable: *A. fatua* shoot biomass				
Fixed factors:	$\chi 2$	Df	p-value	
Soil substrates ABC	10.949	2	0.004	**
Random effects:	Variance	Standard deviation		
T. resupinatum density	0.000	0.006		
Replicate	0.000	0.000		
Residual	0.000	0.008		
Number of observations: 54	Groups: *T. resupinatum* density, 4; Replicate, 3			

Table 14. *Analysis of variance (Anova) on GLMM with response variable* A. sativa *shoot height (DAS 42, soil substrate A) and fixed factor A. fatua density.*

Response variable: *A. sativa* shoot height (DAS 42)				
Fixed factors:	$\chi 2$	Df	p-value	
A. fatua density	23.561	2	<0.001	***
Random effects:	Variance	Standard deviation		
Window	376.77	19.41		
Replicate	14.59	3.82		
Residual	2062.04	45.41		
Number of observations: 135	Groups: Window, 17; Replicate, 3			

Table 15. *Analysis of variance (Anova) on GLMM with response variable* A. sativa *shoot height (DAS 42, soil substrate B) and fixed factor A. fatua density.*

Response variable: *A. sativa* shoot height (DAS 42)				
Fixed factors:	$\chi 2$	Df	p-value	
A. fatua density	18.698	4	<0.001	***
Random effects:	Variance	Standard deviation		
Window	687.4	26.22		
Replicate	0.001	0.033		
Residual	1219	34.91		
Number of observations: 135	Groups: Window, 22; Replicate, 3			

Table 16. *Analysis of variance (Anova) on GLMM with response variable* A. sativa *shoot height (DAS 42, soil substrate C) and fixed factor A. fatua density.*

Response variable: *A. sativa* shoot height (DAS 42)				
Fixed factors:	$\chi 2$	Df	p-value	
A. fatua density	9.163	4	0.057	.
Random effects:	Variance	Standard deviation		
Window	847.7	29.11		
Replicate	140.2	11.84		
Residual	925.6	30.42		
Number of observations: 135			Groups: Window, 22; Replicate, 3	

Table 17. *Analysis of variance (Anova) on GLMM with response variable* A. sativa *development stage (BBCH) and fixed factors* A. fatua *density and Days after sowing (DAS).*

Response variable: *A. sativa* BBCH				
Fixed factor:	$\chi 2$	Df	p-value	
A. fatua density	26.252	4	<0.001	***
DAS	69516.632	5	<0.001	***
A. fatua density:DAS	143.862	20	<0.001	***
Random effects:	Variance	Standard deviation		
Window	0.0059	0.0765		
Replicate	0.0024	0.0486		
Residual	0.1112	0.3335		
Number of observations: 3224			Groups: Window, 36; Replicate, 3	

Table 18. *Analysis of variance (Anova) on GLMM with response variable* A. sativa *shoot chlorophyll content (SPAD) and fixed factor* A. fatua *density and Soil substrate.*

Response variable: *A. sativa* SPAD				
Fixed factor:	$\chi 2$	Df	p-value	
A. fatua density	21.40	4	<0.001	***
Soil substrate	1.310	2	0.520	
A. fatua density:Soil substrate	17.21	8	0.028	*
Random effects:	Variance	Standard deviation		
Window	3.281	1.811		
Replicate	0.595	0.771		
Residual	11.584	3.404		
Number of observations: 405			Groups: Window, 36; Replicate, 3	