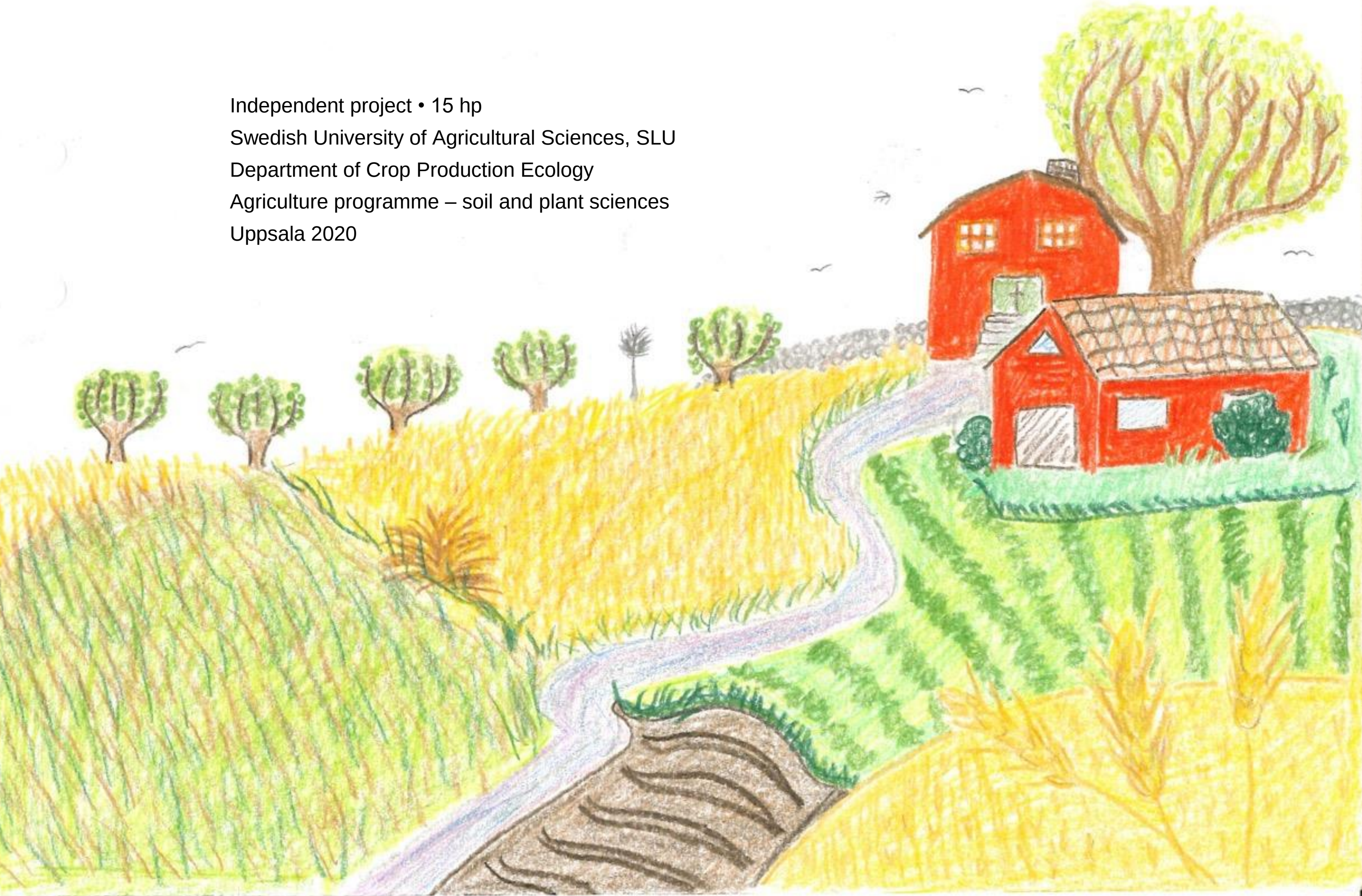
Arbuscular mycorrhiza in landrace and modern wheat

– Its impact on plant performance and how it is influenced by plant breeding and modern cropping practices

Klara Li Yngve



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Abstract

Modern agriculture has a negative impact on climate and environment and is challenged by climate change. A transition to a more sustainable, secure and yet high food production is necessary. Landrace cereals attract attention for their ability to sustain nutrient deficiency, drought and harsh climate conditions. Arbuscular mycorrhiza is a common symbiosis with ancient origin between plant roots and fungi. The aim of this thesis is to review the current knowledge on arbuscular mycorrhiza regarding its impact on wheat landrace performance during cultivation, and to understand if arbuscular mycorrhiza in wheat has been affected by breeding and conventional cropping practices. Arbuscular mycorrhiza may contribute to uptake of phosphorous and other nutrients and enhance drought resistance in wheat. However, the response to arbuscular mycorrhiza in plants is highly variable and dependent on genetical and environmental factors and cropping practices. This thesis concludes that the ability of wheat landrace cereals to adapt to nutrient deficiency and drought stress are most likely not dependent on arbuscular mycorrhiza under Swedish conditions. In addition, input of fertilizers reduces the plant responsiveness to arbuscular mycorrhiza, the crop rotation system might favour or disfavour arbuscular mycorrhiza depending on which crops are included, tillage disfavours arbuscular mycorrhizal fungi and fungicides might reduce spore germination. Thus, conventional practices might have a negative impact on arbuscular mycorrhiza in wheat, even though the farmer’s choice of cultivation methods are more important for arbuscular mycorrhiza than the type of cropping system. Finally, it is concluded that more molecular genetic research is needed in order to understand if arbuscular mycorrhiza in wheat has been affected by breeding for conventional cropping systems.

Keywords: Arbuscular mycorrhiza, landrace varieties, modern cultivars, wheat, conventional cropping systems, organic cropping systems

Preface

This thesis is an independent project in biology (15 hp) within the Agriculture programme – soil and plant sciences at the Swedish University for Agricultural Sciences at the Department of Crop production ecology. It is written within the research project *Sustainable organic food from heritage cereal – using history to form the future,* which is interdisciplinary and involves scientists, entrepreneurs and NGOs. Heritage cereals is an interesting and intriguing field since they are a source of both historical knowledge and of solutions for future food production, and I am happy and grateful that my thesis to some extent may contribute to this project. Nevertheless, when I started my project, I knew little about landrace cereals and even less about arbuscular mycorrhiza (the first challenge was to learn how to spell it correctly!). Without prior knowledge of the enormous scope of the subject, it was difficult to put reasonable limits to the thesis; I wanted to cover most issues that may be relevant for Swedish farmers growing landraces, although that is a whole lot. My hope is therefore that this thesis will provide the reader with an overview of the current knowledge on the significance of arbuscular mycorrhiza for landrace and modern wheat, without going into too much detail on each separate aspect.

Klara Li Yngve,
Uppsala, spring 2020

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Abbreviations

AM fungi	Arbuscular mycorrhizal fungi
AM plants	Arbuscular mycorrhizal plants

1. Introduction

Agriculture of today faces great challenges. It is commonly viewed as a major source of greenhouse gas emissions, it causes environmental pollution, overfertilization and loss of genetic diversity (Pretty *et al.* 2010). At the same time, it must feed a growing world population and be adapted to the altered agricultural conditions and more extreme and unpredictable weather events that are predicted to come with climate change (Pretty *et al.* 2010; FAO 2017). Moreover, most agricultural production is dependent on input of fertilizers that are produced from finite and diminishing resources (Cordell *et al.* 2009). To meet these challenges, transition to a more sustainable and climate adapted, and yet high, food production is necessary. This requires action at many levels and involves the choice of cropping systems and which crops to cultivate on a national, regional and local scale (FAO 2017). Today, cereals, especially wheat, compose a major part of the cultivated land in Sweden and worldwide (Mergoum *et al.* 2009; SCB 2018), and cereal landrace varieties attract attention for their stable productivity even under harsh climate conditions, low soil fertility and drought stress. (Newton *et al.* 2010). These properties are interesting both for breeding of more climate robust cultivars and for cultivation in organic and traditional small-scale cropping systems (Wolfe *et al.* 2008). There are many different factors that influence the yield of both landraces and modern cultivars. This thesis will focus on arbuscular mycorrhiza, and to what extent this common symbiosis between fungi of the phylum *Glomeromycota* and the root systems of plants, affect the performance of landraces and modern cultivars during cultivation and if it can contribute to a sustainable production.

1.1. Background

1.1.1. The origin of agriculture and landrace cereals

Agriculture emerged with the cultivation of cereals more than 10 000 years ago within an area in the Eastern Mediterranean and Asia Minor, known as the Fertile Crescent. This led to the transformation of hunter-gatherer communities into farming communities and the further importance of this process for mankind is hard to overestimate (Salamini *et al.* 2002). From the Fertile Crescent, where species of wild grass were originally domesticated during thousands of years, ancient cereals were spread throughout the world. They adapted to new environments and cropping systems through natural and human selection pressures, unique to each local, resulting in a countless number of landraces (Newton *et al.* 2010).

1.1.2. The shift from landraces to cultivars and the development of conventional and organic cropping systems

Agricultural production was composed of landrace cereals until the emergence of formal plant breeding in the nineteenth century. Since then, landraces have been gradually replaced by a continuous release of new varieties, often called cultivars, developed by progressing breeding techniques (Villa *et al.* 2005; Wouw *et al.* 2010). There are both older and more modern varieties of landraces, and early cultivars differ from more recent cultivars since the methods of plant breeding were and still are continuously advancing. Hence, the discrimination of landrace varieties and cultivars are not always clear (Wiking Leino 2017). Yet, plant breeding has always been focused on just a few goals and above all on increased grain yield, enhanced disease resistance and industrial baking quality (Mergoum *et al.* 2009). This has substantially reduced the genetic diversity of cultivars compared to landraces and also changed genetic and physiological traits (Wouw *et al.* 2010). The production of new, high yielding cultivars during the twentieth century was accompanied and enabled by new agricultural technologies and perhaps most important, the development of inorganic fertilizers and pesticides, which form the basis of the intensive, conventional cropping systems of today (Austin 1999; Morgan & Murdoch 2000). Thus, conventional measures make it possible to grow genetically homogenous cultivars that are predominantly bred for high yield (Morgan & Murdoch 2000; Newton *et al.* 2010; Pérez-Jaramillo *et al.* 2016; Wiking Leino 2017).

In contrast to cultivars, landraces often lack formal crop improvement, are often genetically diverse and continuously and uncontrollably changing due to natural and human selection (Villa *et al.* 2005). They are commonly adapted to pre-industrial farming systems with limited abilities to add fertilizers and handle pests and weeds, lack of drainage and irrigation systems and lack of modern tillage techniques, resulting in more fluctuating and uncontrollable growing conditions compared to conventional cropping systems (Villa *et al.* 2005; Newton *et al.* 2010; Pérez-Jaramillo *et al.* 2016). Due to the inherent heterogeneity in landraces, at least some genotypes in the variety will usually manage biotic and abiotic stress, which guarantees a stable yield over time (Newton *et al.* 2010; Pérez-Jaramillo *et al.* 2016; Wiking Leino 2017).

Limited access to fertilizers and limited control of pests and weeds are also features of organic cropping systems. Therefore, landraces are particularly interesting to grow for organic farmers and for breeding new cultivars suitable in organic cropping systems (Wolfe *et al.* 2008). Organic farming developed simultaneously with conventional agriculture, much as a reaction to the use of hazardous pesticides and finite resources. From being rather marginalized, organic cropping is today predominantly regarded as important for the sustainable development of agriculture (Vogt 2007; European Commission 2014; Näringsdepartementet 2017). Yet, modern cultivars developed specially for organic farming are uncommon and many organic farmers have to grow varieties produced for conventional cropping systems (Wolfe *et al.* 2008).

1.1.3. The terms “modern cultivar” and “modern agriculture”

Most literature referred to in the paragraph above use one or more of the terms “modern breeding”, “modern cultivars”, “modern cereal crops”, “modern varieties” “modern agriculture” and “modern agricultural practices”. Yet, I have found no definition of what “modern” is. How recently must a cultivar have been released in order to be considered modern? What measures are included in modern agriculture? These are questions which very well could be the starting point for yet another thesis. In this thesis, I will use the term “modern” for cultivars released during the last 50 years and the terms “old” or “early” for all other cultivars, released before that/older than 50 years. In the definition of “modern agriculture”, I will include both conventional and organic cropping systems that use techniques and take measures that have been developed during the last century. Other cropping systems will be referred to as “old”. The term “low-input systems”, will be used for systems that do not use pesticides or inorganic fertilizers, including both old cropping systems as well as modern organic systems. Although the definitions may not be widely used, they are used for clarity of the thesis.

1.1.4. Wheat – an ancient and important crop

Wheat is one of the most cultivated crops and one of the most important staple foods in Sweden and worldwide (Mergoum *et al.* 2009; SCB 2018). Moreover, it is likely that wheat was one of the first cereal species to be domesticated. However, wheat is a unifying term for several species with rather different genomes within the genus *Triticum.* The first domesticated varieties of wheat were probably einkorn (*Triticum monococcum* subsp. *monococcum*) that has a diploid genome, and emmer (*Triticum turgidum* subsp. *dicoccum*) that has a tetraploid genome. Einkorn and emmer are today regarded as ancient crops and rarely cultivated (Salamini *et al.* 2002), yet there is a rising interest for these varieties (Wiking Leino 2017). The wheat that is mainly grown today is *Triticum aestivum*, commonly referred to as bread wheat. *T. aestivum* has a hexaploid genome and is thought to be the result of at least two natural crosses of diploid and tetraploid species of grass (Salamini *et al.* 2002). Wheat requires better soil and climate conditions and provide a more unpredictable yield compared to other cereals. Therefore, the cultivation of *T. aestivum* in Sweden was low until the emergence of formal plant breeding and modern cropping systems. Nevertheless, *T. aestivum* has historically been regarded as the most precious cereal because of its white flour and good baking properties. Even though many wheat landraces that once existed in Sweden have been lost, a number of wheat landraces are preserved and still cultivated (Wiking Leino 2017).

1.1.5. Arbuscular mycorrhiza

Arbuscular mycorrhiza is an ancient symbiosis, which has coevolved between plants on land and fungi of the phylum *Glomeromycota*. Arbuscular mycorrhiza is present in 80 percent of all plant families, is widespread in natural ecosystems and is also the most important type of mycorrhiza in agriculture (Gosling *et al.* 2006; Smith & Read 2008a). In spite of extensive research, it is not clear exactly how and to what extent crops benefit from arbuscular mycorrhiza (Smith & Smith 2011). Yet, it appears to be generally accepted that plants acquire P and other growth limiting and often hardly available nutrients from the arbuscular mycorrhiza fungi (AM fungi) in exchange of carbon (C) (Zhu *et al.* 2001; Li *et al.* 2008b; Sawers *et al.* 2008; Neumann & George 2010; Smith & Smith 2011). In addition, the symbiosis is thought to provide the plant with enhanced drought resistance, resistance to pests and diseases and tolerance to heavy metals (Newsham *et al.* 1995; Zhu *et al.* 2001; Li *et al.* 2008b; Sawers *et al.* 2008; Neumann & George 2010; Smith & Smith 2011).

1.2. Aim, hypotheses and research questions

The aim of this thesis is to review the current knowledge on arbuscular mycorrhiza regarding its impact on wheat landrace performance during cultivation and to understand if arbuscular mycorrhiza in wheat has been affected by breeding and conventional cropping practices. The focus of the thesis will be three hypotheses:

1. The ability of landrace cereals to adapt to nutrient limitation and drought is reliant on enhanced nutrient uptake and drought resistance provided by arbuscular mycorrhiza.
2. Agricultural practices in conventional cropping systems disfavour development of arbuscular mycorrhiza.
3. The ability to respond to arbuscular mycorrhiza has been lost in modern cultivars due to breeding for conventional cropping systems.

The following questions are posed in order to investigate the hypotheses:

- Is the ability of landrace cereals to adapt to nutrient deficiency and drought stress dependent on arbuscular mycorrhiza?
- How is arbuscular mycorrhiza affected by input of fertilizers and pesticides, tillage and crop rotation?
- Has the responsiveness to arbuscular mycorrhiza decreased in modern wheat cultivars compared to wheat landrace varieties?

1.2.1. Delimitations

This thesis is limited to the impact of arbuscular mycorrhiza on wheat grown in Sweden, since wheat is one of the most cultivated crops in Sweden and it is of interest to understand the significance of arbuscular mycorrhiza for Swedish agriculture. Accordingly, the focus will be the cultivation of wheat and the significance of mycorrhiza on field scale.

The response to arbuscular mycorrhiza in wheat is dependent on a wide range of factors. In this thesis the focus will be on one factor in the plant: plant root traits, one factor in soil: P levels, as they can also be linked to the use of fertilizers, and three factors in the cropping system that are relevant for the management of mycorrhiza on field scale: tillage, crop rotation and the control of pests and weeds. In addition, the genetic and molecular mechanisms of arbuscular mycorrhiza (partly reviewed by e.g. Sawers et al. (2008)), is important for understanding the interplay between fungi and plant and the impacts of breeding on wheat. Therefore, the genetic and molecular research will be briefly described as well. As a consequence, other factors are excluded, which may limit the discussion and conclusions.

2. Methods

This work is a literature study. The SLU Library search tool, Primo, was used for literature search. The search terms were “mycorrhiza”, “arbuscular mycorrhizal fungi”, “mycorrhiza* spring wheat”, “mycorrhiza*landrace cereal*”, “arbuscular mycorrhiza wheat landrace”, “arbuscular mycorrhiza wheat heritage”, “organic cropping systems history”, “what is modern cultivars” and “arbuscular mycorrhiza crop rotation”. The initial plan was to focus the thesis on spring wheat, however no studies made specifically on spring wheat were found and the focus was therefore broadened to wheat. With this focus, both reviews and experimental studies was identified. A number of studies either investigating the impact of various factors on arbuscular mycorrhiza or comparing landrace varieties with modern cultivars of wheat with respect to agronomic traits were found. However, only three studies except review articles comparing landrace varieties and modern cultivars of wheat with respect to arbuscular mycorrhiza were identified. In addition to the literature search, relevant literature on the subjects of mycorrhiza, landraces and cereal production were also obtained from other sources and from the reference list in *Spannmål – Svenska lantsorter* by Wiking Leino (2017).

3. Results

The result of the literature search is presented in the following order to address the three hypotheses and questions of the thesis:

- impacts of arbuscular mycorrhiza in plants
- different ways to measure the response to arbuscular mycorrhiza in plants
- factors that affect arbuscular mycorrhiza
- traits that discriminate wheat landrace varieties from modern wheat cultivars
- differences between landrace and modern cultivars with respect to mycorrhiza

3.1. Arbuscular mycorrhiza in plants

3.1.1. The building of arbuscular mycorrhiza

AM fungi are obligate biotrophs, and thus unable to grow and complete their life cycle without a host. In symbiosis with the plant, the fungi grow a so called extraradical mycelium (the mycelium existing outside the roots if the host plant) that usually covers a much greater soil volume than the root system of the host plant (Giovannetti *et al.* 2010). Plants can be colonized either by hyphae from germinating spores or by hyphae from already existing mycelium in the soil. The hyphae penetrate, infect and forms arbuscules inside the root cells, where the nutrient exchange takes place. For agricultural crops, an already existing extraradical mycelium in the soil appear to be a faster and more efficient source to colonization of roots than spores (Brito *et al.* 2013). Spore germination only happens when spores receive signals from the roots of a host plant and is also temperature dependent. At temperatures below 18° C, germination is slower or fully inhibited (Giovannetti *et al.* 2010).

3.1.2. Nutrient uptake

There are two ways of nutrient uptake in arbuscular mycorrhizal plants (AM plants): direct uptake through roots and uptake via the AM fungal pathway (Smith

& Read 2008b). Due to the high demand for P in plants combined with the usually poor availability and limited mobility of P in soil, the rhizosphere often becomes a P depletion zone. Fungal hyphae are finer than roots and root hair and reach beyond the rhizosphere. Through the hyphae, the plant can acquire P from the soil solution that is otherwise unavailable to the plant, in exchange for C that the fungi cannot produce itself. However, just a small amount of P in soil exist in the soil solution whereas a high amount of P in soil exist in insoluble forms that are not directly available for uptake neither by hyphae nor by roots (Smith & Read 2008b). Yet, some research indicates that arbuscular mycorrhizal fungi except aiding in P uptake from the soil solution, also enable plants to acquire insoluble P probably due to fungal exudates that solve insoluble P compounds (Smith & Smith 2011). In addition to P, research has shown uptake via the AM fungal pathway of Zn, Ca, Cu, S in the form of SO_4^- and N in the form om NO_3^- and NH_4^+ (Neumann & George 2010).

Lower biomass is often observed in plants colonized by AM fungi, when compared to non-mycorrhizal plants in experimental studies. This is called growth depressions. An established hypothesis is that this is due to imbalance in the C-P-trade and that the symbiosis consequently leans towards parasitism. However, Li et al. (2008a) and Smith and Smith (2011) propose that the growth depressions might depend on P deficiency, since the AM fungi might prevent the direct uptake of P in plants and fail to completely compensate for this. They conclude that the mechanisms in the plant-fungal interaction behind the C-P-trade are predominantly unknown and that the area need more research (Li *et al.* 2008a; Smith & Smith 2011).

3.1.3. Drought resistance and additional benefits of arbuscular mycorrhiza

AM fungal colonisation of wheat roots has been shown to provide a relatively higher enhancement of biomass and grain yield under water deficient than well-watered conditions, indicating that arbuscular mycorrhiza aid in water uptake. The explanation given is that the hyphae explore a greater soil volume and smaller pores in the soil and also adhere to soil particles which further increases the contact with the soil solution (Al-Karaki *et al.* 2004). However, Smith and Read (2008b) state that there is no clear evidence for direct water uptake via fungal hyphae, even though it might exist. Instead, they point out that the transport of water through roots and stomata might be altered in plants grown in soil with much AM fungal hyphae and that this can improve the water relations of the plant. In addition, changes in nutritional status and size of the plant as well as improved soil structure following AM fungal colonization are thought to indirectly contribute to enhanced drought resistance. The plant water relations are apparently altered in many ways by the symbiosis and the exact mechanisms are still not understood (Smith & Read 2008b). Besides nutrient uptake and drought resistance, arbuscular mycorrhiza has in some studies been shown to enhance tolerance of heavy metals and salinity and resistance to pests and diseases and also to contribute to enhanced soil structure (Newsham *et al.* 1995; Smith & Smith 2011).

3.1.4. Measuring response to arbuscular mycorrhiza in plants

In most studies used in this thesis, the plant responsiveness to arbuscular mycorrhiza is measured in biomass and calculated as the difference in biomass between AM plants and non-mycorrhizal plants, divided by the biomass of the non-mycorrhizal plant (see equation 1). The change in biomass is often called growth response (Hetrick *et al.* 1992; Smith & Smith 2011; Lehmann *et al.* 2012). In some studies, the dependence upon mycorrhiza is also calculated, as the difference in biomass between AM plants and non-mycorrhizal plants, divided by the biomass of the AM plant (see equation 2) (Hetrick *et al.* 1992). In some studies, the responsiveness and/or dependence is instead calculated upon tissue P concentration either in roots or shoots or plant P efficiency (see equation 1 and 2) (Zhu *et al.* 2001; Lehmann *et al.* 2012). When comparing the impact of mycorrhiza on different varieties, it is also common to measure percent root colonized by AM fungi and root/shoot ratio (Lehmann *et al.* 2012).

$$Responsiveness = \frac{Biomass\ or [P]\ of\ AM\ plant - Biomass\ or\ [P]\ of\ non{-}AM\ plant}{Biomass\ or\ [P]\ of\ non{-}AM\ plant} \qquad \text{Eq. 1}$$

$$Dependence = \frac{Biomass\ or [P]\ of\ AM\ plant - Biomass\ or\ [P]\ of\ non{-}AM\ plant}{Biomass\ or\ [P]\ of\ AM\ plant} \qquad \text{Eq. 2}$$

3.2. Factors that affect arbuscular mycorrhiza in wheat

The degree of root colonization by arbuscular mycorrhizal fungi and how the plant is affected by the symbiosis depend on many factors. Among these are the compatibility of the genotypes of fungi and plant and plant genomic traits as well as time and speed of root colonization and how the symbiosis changes with the age and development stages of the plant (Hetrick *et al.* 1993; Janos 2007; Li *et al.* 2008a; Lehmann *et al.* 2012; Essiane-Ondo *et al.* 2019). Another important factor is the availability of nutrients in the soil, especially phosphorous and other growth-limiting nutrients (Janos 2007; Smith & Smith 2011). Furthermore, water, temperature and soil pH, tillage, crop rotation system and pest and weed management influence the symbiosis (Smith & Smith 2011). According to the focus of this thesis (see section 1.2.1) this section will describe the significance of plant root traits, P levels in soil, tillage, pest and weed management and crop rotation for arbuscular mycorrhiza. However, the section starts with a short review of the plant and fungal genetic material since this, though beyond the main scope of this thesis, to a great extent determines the AM fungal colonization of roots and the response by the plant. An overview of the effects of the factors presented in this section is presented in table 1.

Table 1. An overview of the factors that affect arbuscular mycorrhiza that are presented section 3.2.

Factor	**Effect on arbuscular mycorrhiza**
Plant genetic material	Compatibility of species of fungi and plant important
Plant root traits	Small and coarse root system → higher mycorrhizal responsiveness Unclear if the mycorrhizal response is correlated with the degree of root colonization
P levels in soil	In general, decreased positive response with increased P levels in soil
Weeds and crop rotation	Mycorrhizal crops and weeds previous to wheat cultivation enhance mycorrhizal colonization and responsiveness
Tillage and weed control	Tillage negatively affects mycorrhizal fungi; herbicides can alter the fungal community
Fungicides	Can affect spore germination and colonization of roots positively and negatively depending on which fungicide that are used

3.2.1. Plant genetic material

Both the species of fungi and the variety and genotype of a plant affect the arbuscular mycorrhizal symbiosis, which can range from parasitic to mutualistic (though it must be stressed that a seemingly parasitic interaction might benefit the plant by means that research yet cannot measure or explain (Janos 2007; Smith & Smith 2011). The diverging compatibilities of fungus and plant were, for example, apparent in a greenhouse experiment by Hetrick et al. (1992). They tested the response to ten fungal species on one species of native grass, one landrace variety and two modern cultivars of wheat. The degree of root colonization and responsiveness by each variety to each inoculum clearly differed from one another. The landrace variety responded positively to most fungi, whereas the modern cultivars only responded by growth depression or showed no significant response at all (Hetrick *et al.* 1992). However, in a review article on the significance of arbuscular mycorrhiza in crops, Smith and Smith (2011) concluded that even though the importance of the species of the symbionts are apparent, the mechanisms behind the combability of plant and fungi are still largely unknown.

3.2.2. Plant root traits

Plant root traits e.g. root length, branching, fineness and building of root hairs seem to be of particular importance for arbuscular mycorrhiza. In a review article, Smith and Smith (2011) state that it is well established that varieties with a small and coarse root system have higher positive response, in terms of increased biomass, to AM fungi under P deficient conditions compared to plants with extensive root system and more root hair. This is supported by a study by Hetrick et al. (1992), in which the mycorrhizal response in wheat, decreased with increased branching of the plant root systems.

It is not clear whether the degree of root colonization is correlated with the response by the plant. Hetrick et al. (1992) found no relationship between growth response and root colonization when testing ten individual species of fungi on one landrace and two modern cultivars of wheat in a pot culture study. However, in a contradictory study, improvement of shoot biomass and P content were consistent with greater root colonization in a pot culture experiment on modern wheat cultivars by Brito et al. (2013). Lekberg and Koide (2005) and Lehmann et al. (2012) also found a positive relationship between percentage colonized roots and mycorrhizal growth response in their meta-analyses of former studies on arbuscular mycorrhizal influence on plants. Lehmann et al. (2012) point out that these results oppose the findings of Hetrick et al. (1992) as well as consistent results from one study on wild emmer and one on maize, but argue that their own findings and the study of Lekberg & Koide are more reliable since they are made upon 400 and 290 trials, respectively, while the other studies were made on around 30 trials each. However, their findings are based on studies on various crops including cereals, vegetables and legumes.

3.2.3. P levels in soil

Landraces of wheat are adapted to various low input systems whereas modern cultivars are adapted to more intense, high input conventional cropping systems. One important difference between these systems is the availability of nutrients, including the availability of phosphate which is often deficient in low input systems while sufficient in conventional cropping systems due to input of inorganic fertilizers (Wolfe *et al.* 2008). The meta-analysis of Lehmann et al. (2012) showed no correlation between P concentrations in the soil and the responsiveness to mycorrhiza by the plants. However, Lehmann et al. (2012) point out that the meta-analysis contained a low number of studies (8 out of 39) in which P concentration was a factor, which makes the results less reliable. Furthermore, a greenhouse study that investigated the impact of AM fungi on the growth of wheat cultivars under different levels of P in the soil (Hetrick *et al.* 1996) showed that the responsiveness decreased with increased P concentrations. This is consistent with the meta-analysis of 290 trials determining the effects of a range of agricultural practices on mycorrhizal colonization and responsiveness, which showed that the colonization by AM fungi was less likely to increase plant biomass if the P supply was high (Lekberg & Koide 2005). A common explanation for why the positive response weakens with increased P levels is that there is then sufficient P in the rhizosphere for direct uptake by plant roots (Smith & Smith 2011). However, even when there is no net response or a negative response to arbuscular mycorrhiza in the plant (indicating that the plant acquires enough P via direct uptake), the plant might still take up P via the AM fungal pathway. This has been shown in greenhouse experiments by tracking of radioactive P and findings of active AM-specific P transporter genes in cortex cells in AM plant roots (for example, one study is conducted by Li et al. (2008a) and more studies are reviewed by Smith & Smith (2011)). Since this uptake is not contributing to any measurable positive mycorrhizal response, it is yet unclear in what way this uptake affects the plant (Li *et al.* 2008a; Smith & Smith 2011).

3.2.4. Weeds and crop rotation

Since arbuscular mycorrhizal fungi are biotrophic, they need a living host plant in order to develop and maintain their extraradical mycelial network in soil. Brito et al. (2013) showed in a pot culture study that the growing of weeds prior to wheat led to early colonization of the wheat roots, and that the plants in these pots later on had higher shoot biomass and P content. Hereby, it was concluded that the weeds amplified the extraradical mycelial network and thus provided a more effective colonization. Likewise, a number of studies on crop rotation and maize have shown that if the previously cultivated crop form arbuscular mycorrhiza, the mycorrhizal colonization, growth and P uptake of succeeding crops increases. If the previous crop is non-mycorrhizal, such as oil seed rape and other species of the *Brassicaceae* family, the amount of AM fungi in soil decreases which leads to reduced colonization and growth of the succeeding crop (for references, see e.g. (Karasawa & Takebe 2012)). In addition, mycorrhizal cover crops cultivated along with non-mycorrhizal crops have been shown to positively affect the growth of succeeding maize and wheat (Karasawa & Takebe 2012). Some studies, e.g. (Brito *et al.* 2012) and (Arihara & Karasawa 2000), indicate that wheat are less responsive to arbuscular mycorrhiza than crops such as maize and triticale, and thus less suitable as previous crop.

3.2.5. Tillage and weed control

A field trial study on wheat showed that tillage reduced colonization relative to a no-till system (Brito *et al.* 2012). Likewise, soil disturbance simulating mechanical weed control resulted in less colonization compared to the use of herbicides (Brito *et al.* 2013). Most likely, soil disturbance such as tillage disrupt the extraradical mycelial network and consequently the rate and degree of colonization (Brito *et al.* 2012, 2013). The effect of different herbicides on AM fungi has also been investigated. For example, Dodd and Jeffery (1989b) found that the effect on spore germination and colonization ranged from positive to negative depending on which herbicide that was used. Another study found no effect of the systemic glyphosate and the contact-acting paraquat on the degree of root colonization, however the plant response following the colonization were significantly greater after Glyphosate than after Paraquat (Brito *et al.* 2013). The suggested explanation given to that was that Paraquat might alter the AM fungal community in the soil in a negative manner.

3.2.6. Fungicides

A pot culture greenhouse study investigated the effect of five different fungicides on three species of arbuscular mycorrhizal fungi inoculated on wheat plants (Dodd & Jeffries 1989a). The most common reaction by the AM fungi was reduced spore germination, however one fungicide stimulated increased AM colonization of wheat roots. The increased colonization was also found in a study by von Alten et al. (1993). The reduced spore germination is perhaps not as surprising as the positive effect of one of the fungicides. Two possible explanations given in the studies are that the fungicide might increase exudation of soluble sugars to the AM fungi, and the unlikeliness of transportation of foliar applied fungicides into the roots, thus not affecting the fungal-root symbiosis. However, both studies conclude that different fungicides have different modes of action and thus affect the AM fungal community differently (Dodd & Jeffries 1989a; von Alten *et al.* 1993).

3.3. Landrace varieties and modern cultivars of wheat

3.3.1. What traits distinguish landrace varieties from modern cultivars of wheat?

Although belonging to the same species, both landraces and cultivars of wheat differ greatly in their physiological traits and there are considerable differences within both groups, especially among landrace varieties (Lehmann *et al.* 2012). However, each group also has common traits that enable a discrimination of landrace varieties and modern cultivars. In a comparative study of 57 Nordic spring wheat cultivars and 22 Nordic landraces, landraces were in general earlier in heading and maturity, a lot taller, more inclined to lodging and had less grains per spikelet than modern cultivars (Diederichsen *et al.* 2013). A plant can respond to environmental fluctuations by changing root architecture and root to shoot ratio within the limits of its genotype and breeding for high yielding cultivars has affected the genotype of shoot and roots traits in cereals (Bektas 2015). Comparative pot culture studies on landrace varieties and modern cultivars of wheat showed that the total root biomass and both shallow and deep roots are larger in wheat landraces than in modern wheats (Waines & Ehdaie 2007; Bektas *et al.* 2016). Not surprising and consistent with the major breeding objective, several studies show that modern cultivars generally produce higher grain yield than landrace cereals (Diederichsen *et al.* 2013; Konvalina *et al.* 2014; Hlisnikovský *et al.* 2019). Due to the higher yield production, modern cultivars have a higher nutrient demand and are more susceptible to nutrient deficiency than landrace varieties (Lehmann *et al.* 2012).

3.3.2. Differences between landrace cereals and modern cultivars with respect to arbuscular mycorrhiza

The degree of colonization and the benefit or cost in terms of biomass and yields differs greatly between wheat cultivars and the studies that compare landrace and modern wheat are contradictive (Brito *et al.* 2013). An overview of the studies and their main results presented in this section is presented in table 2.

Table 2. An overview of the main results of the studies presented in section 3.3.2. All studies were conducted on wheat except Toth et al. 1990, that were conducted on maize.

Study	**Type of study**	**Responsiveness to mycorrhiza in landrace and modern cultivars**
Toth *et al.* 1990	Field trials	Roots of modern maize cultivars with resistance to fungal pathogens were less colonized than roots of modern maize cultivars lacking resistance to fungal pathogens
Hetrick *et al.* 1992	Greenhouse pot experiment	Greater growth response and dependence in landraces and old cultivars than in modern cultivars

Zhu *et al.* 2001	Greenhouse pot experiment	Greater response calculated on P tissue concentrations in old cultivars than in modern cultivars
Lehman *et al.* 2012	Meta-analysis	No difference in responsiveness between landraces and modern cultivars

In the study by Hetrick et al. (1992) the greatest response was found in landraces, followed by old cultivars. Modern cultivars responded the least and were also less dependent on arbuscular mycorrhiza than landraces. In one experiment in the study, ten species of fungi were tested on one landrace variety and two modern cultivars. Eight species of fungi stimulated growth in the landrace variety whereas six species of fungi caused growth depression in one or both of the modern cultivars, and no positive growth response was observed. Upon these results, Hetrick et al. (1992) hypothesized that the frequency of genes that stimulate arbuscular mycorrhizal symbiosis might have been reduced by breeding for high input agriculture, since the metabolic cost of the symbiosis would outweigh the benefit of the nutrient uptake via AM under fertilized conditions (Hetrick *et al.* 1992).

In order to test if modern breeding practices has affected P uptake efficiency and responsiveness, Zhu et al. (2001) tested the influence of arbuscular mycorrhiza on percent colonization, root and shoot ratio and biomass and tissue P concentration on four old wheat cultivars, released between 1860 and 1955, and two modern wheat cultivars released 1991 and 1996. The results showed that the tissue P concentrations were higher in the old cultivars and that the responsiveness, calculated on the P concentrations, decreased with the year of release of the cultivar. For root and shoot ratio, biomass and percent root colonization, no trends were detected.

In contrast to these two studies, a meta-analysis of 242 trials on mycorrhizal responsiveness in terms of total dry weight in wheat, performed between 1981 and 2010 showed no significant difference between mycorrhizal responsiveness in landraces and cultivars of wheat released after 1950 (Lehmann *et al.* 2012). A study on maize found that modern cultivars that were bred for resistance to fungal pathogens were less colonized by AM fungi than modern cultivars susceptible to fungal pathogens. It suggests that breeding for disease resistance may reduce mycorrhizal colonization levels (Toth *et al.* 1990).

4. Discussion

4.1. Is the ability of landrace cereals to adapt to nutrient deficiency and drought stress dependent on arbuscular mycorrhiza?

There are clear evidences that arbuscular mycorrhiza can contribute to nutrient uptake and drought tolerance in different varieties of wheat, since arbuscular mycorrhiza can enhance uptake of P and other nutrients from the soil solution, release insoluble forms of P into the soil solution and alter plant water relations, although several of the mechanisms involved are not fully revealed (Newsham *et al.* 1995; Al-Karaki *et al.* 2004; Smith & Read 2008b; Smith & Smith 2011). However, there are also data indicating that the ability of wheat landrace varieties to adapt to nutrient limitation and drought stress may also be due to their development of large and branched root systems, which contributes to both water and nutrient uptake (Lehmann *et al.* 2012). In addition, it has been shown that plants with smaller root systems benefit more from arbuscular mycorrhiza compared to plants with more developed root systems (Smith & Smith 2011). With this in mind it could be speculated that modern cultivars are perhaps more dependent on the nutrient and water uptake via the AM fungal pathway than are wheat landraces. However, this is contradicted by the result by Hetrick et al. (1992) which showed a decreased dependence on mycorrhiza in modern wheat cultivars.

In conclusion, arbuscular mycorrhiza is most likely not pivotal for the ability of wheat landraces to adapt to nutrient and water deficient conditions although it might contribute to these abilities provided that the wheat variety and AM fungi are compatible, and the cropping practices are favourable for root colonization and plant response. Instead, the more developed root architecture of landrace cereals is probably of greater importance for nutrient uptake and drought resistance. In addition, it seems unlikely that nutrient uptake and water relations, two fundamental functions in plants, would be dependent on a symbiosis that are influenced by various environmental factors and probably not as reliable as root traits. However, the contribution of mycorrhiza to drought resistance is probably more important in semi-arid areas (Al-Karaki *et al.* 2004) than in Sweden since most parts of Sweden have a humid climate and are not frequently exposed to drought. In addition, spore germination are probably disfavoured by the relatively cold climate in Sweden, since spore germination are reduced at temperatures below 18° C (Giovannetti *et al.* 2010) (although not investigated, it is possible to speculate that the species of AM fungi native to Swedish soils are adapted to the Swedish climate). Yet, the summers in Sweden are predicted to become drier and warmer as a consequence of global warming (Bernes 2016). Thus, it could be speculated that that the importance of mycorrhiza for Swedish agriculture may increase.

4.2. Do agricultural practices in conventional cropping systems have a negative impact on arbuscular mycorrhiza in wheat?

In this thesis, modern farming systems include both conventional and organic agriculture. Wolfe et al. (2008, p. 325) conclude that “it is likely that there are almost as many organic farming systems as there are organic farmers”. Even though conventional cropping systems in Sweden are probably more homogenous than the organic, due to the use of inputs, they still vary with local climate, soil and not least the farmer’s choice of cultivation practices. Hence, when studying the impact of modern cropping systems on arbuscular mycorrhiza in wheat it seems relevant and important to discuss the impact of the following different cultivation methods and their influence on arbuscular mycorrhiza; Input of fertilizers, crop rotation and tillage and control of weeds and pests.

Input of fertilizers

Increased P levels in soil will most likely decrease the responsiveness to arbuscular mycorrhiza by the plant. This was shown both in the greenhouse study by Hetrick et al. (2006) and in the meta-analysis by Lekberg & Koide (2005). Although there is an opposing result published by Lehman et al. (2012), it is less reliable since P levels were controlled in only 8 of the 39 studies included in their meta-analysis. Input of inorganic fertilizers increases the levels of plant available P in soil and promotes direct uptake by the plant (given that the nutrients added are not too tightly bound to the soil or lost through leakage) (Eriksson *et al.* 2011). Hence, the high input of fertilizers in conventional cropping systems may reduce the beneficial effects of arbuscular mycorrhiza.

Crop rotation

Arbuscular mycorrhiza are enhanced by cultivation of mycorrhizal previous crops (Karasawa & Takebe 2012). Thus, management of the cropping system as whole and not only of each single crop are important for the promotion of arbuscular mycorrhiza. Wheat may not be a favourable previous crop for enhancing mycorrhiza (Arihara & Karasawa 2000; Brito *et al.* 2012). Thus, conventional systems, in which wheat are often cultivated two or three years in a row, are probably unfavourable. In organic cropping systems, a well-planned crop rotation is fundamental for controlling pests and weeds (Wolfe *et al.* 2008) and it is possible to speculate that this would favour arbuscular mycorrhiza. Yet, in essence it is the choice of crops and eventual cover crops in the crop rotation that are important for arbuscular mycorrhiza, and not the type of cropping system.

Tillage and control of weeds and pests

Tillage has a negative impact on arbuscular mycorrhiza, due to the disruption of the extraradical mycelial network (Brito *et al.* 2012). Different tools for breaking up the soil and for weed control have probably been used since the emergence of agriculture and the plough was introduced to Swedish agriculture in the 17th century (Fogelfors 2015), which implies that some disturbance of the mycelial network has always occurred. However, tillage in organic and conventional cropping systems of today are conducted by strong machines. It is possible that this makes the disturbance more severe. Moreover, organic systems are in general more dependent on tillage for weed and pest control than conventional systems, since they lack the possibility to use chemical pesticides (Fogelfors 2015). The use of herbicides for weed control is less destructive for arbuscular mycorrhiza than are tillage (Brito *et al.* 2013). Thus, the dependence on tillage in organic farming may disfavour AM fungi. On the other hand, the limited abilities to control weeds in organic farming result in more weeds in the fields. This could promote arbuscular mycorrhiza since the presence of weeds in fields before cultivation of wheat has a positive impact on arbuscular mycorrhiza (Brito *et al.* 2013). The use of fungicides either reduces spore germination or promoted root colonization depending on which plant protection product that was used (Dodd & Jeffries 1989a; von Alten *et al.* 1993). None of the fungicides tested in the studies reviewed for this theses are approved in Sweden (Jordbruksverkets växtskyddscentraler 2020) and it would be interesting to investigate the impact of pesticides that are commonly used in Sweden today.

4.3. Has the ability to respond to arbuscular mycorrhiza been lost in modern cultivars due to breeding for conventional cropping systems?

The literature search resulted in only three articles that compared modern wheat cultivars with wheat landraces with respect to arbuscular mycorrhiza. Two of the studies did not only include landraces of *T. aestivum* but also diploid and tetraploid wheat landrace varieties and one of the studies included only early cultivars released between 1860 and 1955 but no wheat landrace varieties. Since all three studies contained diploid and tetraploid wheats or old cultivars, the discussion on the last hypothesis - *The ability to respond to arbuscular mycorrhiza has been lost in modern cultivars due to breeding for conventional cropping systems* - is focused on wheat landrace varieties in general and not only on *T. aestivum*, which is also relevant due to the rising interest for landraces in general.

The results of Hetrick et al. (1992) and Zhu et al. (2001) showed a decrease in plant responsiveness to arbuscular mycorrhiza with the year of release. Both suggested that modern breeding unintentionally has selected for low responsiveness to arbuscular mycorrhiza, probably because the benefit of the symbiosis is less than the cost in conventional fertilized cropping systems. However, this reasoning is opposed in a review article on arbuscular mycorrhizal research by Sawers et al. (2008). Indeed, they acknowledge the results of Hetrick et al. showing that the modern cultivars were less mycorrhizal dependent than the landraces. However, Sawers et al. phrase that dependence is the degree of ability to function without arbuscular mycorrhiza, and that this is determined solely by plant traits, whereas the capacity to benefit from the symbiosis is based on the fungal-plant interaction, and that both the dependence on mycorrhiza by a plant and the capacity by a plant to benefit from mycorrhiza affect the measured responsiveness. Upon this, Sawers et al. argue that the smaller responsiveness in modern cultivars measured by Hetrick et al. was probably due to their decreased dependence on mycorrhiza, rather than a loss of ability to respond to mycorrhiza. Sawers et al. further states that the reduction in dependence in the modern wheat cultivars was due to their increased ability to acquire P without arbuscular mycorrhiza. However, the basis for this statement is not clear. In addition, the smaller root system of modern wheat cultivars would rather indicate an increase in dependence since plants with small root systems tend to benefit more from mycorrhiza.

In essence, Hetrick et al. (1992) and Sawers et al. (2008) represent two different hypotheses:

- The responsiveness to mycorrhiza is a genetic trait that has decreased in modern wheat cultivars through breeding
- Modern wheat cultivars still possess the ability to respond to mycorrhiza. However, they have become less dependent on mycorrhiza, and thus respond to a lesser degree.

The result of Lehman et al. (2012) showed no differences in the responsiveness to arbuscular mycorrhiza between wheat landraces and modern cultivars, which supports the hypothesis that the modern cultivars still possess the ability to respond to arbuscular mycorrhiza. However, one of the major breeding goals for modern cultivars have been disease resistance and the results of Toth et al. (1990) may indicate that cultivars with fungal pathogen resistance are less likely to be colonized by arbuscular mycorrhiza. If this is true, it supports the hypothesis that the genetic traits that control arbuscular mycorrhiza in wheat has been altered by breeding. Yet, the authors stress that the indication was unsure. In addition, the study was conducted on maize and thus the relevance for wheat is uncertain. In conclusion, it is not clear if the ability to respond to arbuscular mycorrhiza has been lost in modern cultivars due to breeding for conventional cropping systems. To answer this, more research is needed, especially on the genetic mechanisms behind arbuscular mycorrhiza. Although not included in this thesis, there are several studies with molecular approaches for the identification of variation in plant responsiveness to arbuscular mycorrhiza (see references in e.g. Sawers et al. (2008)).

4.4. Conclusions and further research

Based on the results discussed in this thesis, it can be concluded that root traits are probably more important for the ability of wheat landrace varieties to adapt to nutrient and water deficiency than arbuscular mycorrhiza under Swedish conditions, even though the importance of arbuscular mycorrhiza might increase when the Swedish summers become dryer. High input of fertilizers probably enhances the direct plant uptake of P which decreases the dependence and response to mycorrhiza. Choice of cultivation practices such as tillage, weed control and crop rotation is more important for the management of AM fungi on field scale than if the cropping system is organic or conventional. To understand if breeding has negatively affected the responsiveness to mycorrhiza in modern cultivars, more research on molecular genetic level is needed. Based on the evidence reviewed here, it could be suggested that arbuscular mycorrhiza is not of significant importance for wheat landrace performance in Swedish agriculture. However, since the symbiosis can contribute to enhanced nutrient uptake and drought resistance it could be interesting to further investigate how agricultural practices on field scale could be developed in order to promote the responsiveness to mycorrhiza and which wheat varieties and other agricultural crops that are most likely to show high response to AM fungi existing in Swedish soils.

However, to conduct studies on arbuscular mycorrhiza is complicated. As already discussed, the AM fungal colonization of roots and the responsiveness to arbuscular mycorrhiza are influenced by many factors. It is difficult, if not impossible, to conduct experiments that investigate all these factors, but it is also difficult to conduct experiments that with certainty exclude other factors than those that are intended to be investigated, especially in field trials (Lehmann *et al.* 2012).

Greenhouse pot studies are common for studies on mycorrhiza, since this enable a better control of different parameters than field trials. For example, in pot culture studies it is possible to have non-mycorrhizal pots for negative control. However, growing in pots, that are often small, can affect the root morphology of the plants, which in turn might affect the AM fungal colonization and plant responsiveness (Zhu *et al.* 2001). Moreover, the measured responsiveness will alter depending on environmental conditions, such as P levels in soil. Different varieties will show maximal responsiveness at different conditions (Sawers *et al.* 2008). Also, the time, speed and duration of colonization differs between varieties and influence the responsiveness and when it is at its maximum. This makes it difficult both to decide whether a plant variety is responsive or not and above all to make comparisons between two or more varieties. For relevant comparisons between varieties as well as between mycorrhizal and non-mycorrhizal plants, the time for measuring biomass should probably not be the same for all varieties (Janos 2007).

In conclusion, the three hypotheses are addressed with the following short answers:

- The ability of wheat landrace cereals to adapt to nutrient deficiency and drought stress are most likely not dependent on arbuscular mycorrhiza under Swedish conditions.
- Input of fertilizers reduces the plant dependence and responsiveness to arbuscular mycorrhiza, the crop rotation system might favour or disfavour arbuscular mycorrhiza depending on which crops are included, tillage disfavours AM fungi and fungicides might reduce spore germination. Thus, conventional practices might have a negative impact on arbuscular mycorrhiza in wheat, even though the farmer’s choice of cultivation methods are more important for arbuscular mycorrhiza than type of cropping system.
- More molecular genetic research is needed in order to answer if the ability to respond to arbuscular mycorrhiza has been lost in modern cultivars due to breeding for conventional cropping systems.

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