Soil Biology & Biochemistry 84 (2015) 210–217

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Responses of wheat to arbuscular mycorrhizal fungi: A meta-analysis of field studies from 1975 to 2013

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ARTICLE INFO

Article history:
Received 29 October 2014
Received in revised form
16 February 2015
Accepted 18 February 2015
Available online 4 March 2015

Keywords:
AMF root colonization
Field-grown wheat
Grain yield
Meta-analysis
Mycorrhizal field inoculation
Nutrient uptake

ABSTRACT

Arbuscular mycorrhizal fungi (AMF) can benefit growth and yield of agriculturally significant crops by increasing mineral nutrient uptake, disease resistance and drought tolerance of plants. We conducted a meta-analysis of 38 published field trials with 333 observations to determine the effects of inoculation and root colonization by inoculated and non-inoculated (resident) AMF on P, N and Zn uptake, growth and grain yield of wheat. Field AMF inoculation increased aboveground biomass, grain yield, harvest index, aboveground biomass P concentration and content, straw P content, aboveground biomass N concentration and content, grain N content and grain Zn concentration. Grain yield was positively correlated with root AMF colonization rate, whereas straw biomass was negatively correlated. The most important drivers of wheat growth response to AMF were organic matter concentration, pH, total N and available P concentration, and texture of soil, as well as climate and the AMF species inoculated. Analysis showed that AMF inoculation of wheat in field conditions can be an effective agronomic practice, although its economic profitability should still be addressed for large-scale applications in sustainable cropping systems.

1. Introduction

Arbuscular mycorrhizal fungi (AMF, phylum Glomeromycota, Schüßler et al., 2001) are beneficial microbes, ubiquitous in natural and agricultural ecosystems. AMF establish a symbiosis with the majority of indigenous and cultivated plant species in terrestrial environments, supplying mineral nutrients to the plants in exchange for photosynthetically fixed carbon (Smith and Read, 2008). The fungi increase plant growth and uptake of P, N, S, K, Ca, Fe, Cu and Zn that are absorbed and translocated by the extraradical mycelial network spreading from colonized roots through the bulk soil. Other AMF beneficial effects include host plants' increased resistance to biotic (pathogens) and abiotic stress (drought, salinity, heavy metals) and increased soil quality by enhancing soil aggregation and improving structure (Newsham et al., 1995; Augé, 2001; Rillig and Mummey, 2006; Bedini et al., 2009).

Much of the knowledge about AMF functions is derived from laboratory experiments, in which plants are inoculated with different fungal species or isolates in sterilized soil, to exclude the presence of indigenous AMF that could influence plant response or compete with inoculated AMF (e.g., Klironomos, 2000; Munkvold et al., 2004). Soil sterilization minimizes the abundance of decomposers and pathogens, thus reducing the functional complexity of the soil biological community. Soil microbial filtrates are commonly supplied to the experimental pots to mimic the field environment and to make experimental conditions uniform (van der Heijden et al., 2003; Avio et al., 2006). Nevertheless, results obtained from these experiments are not directly relevant to the field where other kinds of soil organisms interact with plants and AMF, and where plant inter- and intraspecific competition for light, water and nutrients occurs (Pringle and Bever, 2008; Pellegrino et al., 2011). Therefore, the recommendations based on such experiments may lack agronomic relevance.

McGonigle (1988) and Lekberg and Koide (2005) reviewed published field trials with crop plants inoculated with AMF and observed that higher root colonization, due to inoculation, was positively correlated with crop yield and P uptake, which increased more than 30%. Treseder (2013), conducting a meta-analysis of laboratory and field-based trials on several plant species (e.g., C3 grass and C4 grass), confirmed the association between colonized root length and plant growth and P content, which explained 12% and 25% of the variability in biomass and P effect sizes, respectively.

The effect on biomass and nutrient uptake mediated by AMF varies widely among plant species and even among plant genotypes (Klironomos, 2000; Lehmann et al., 2012). According to their

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http://dx.doi.org/10.1016/j.soilbio.2015.02.020
0038-0717/

responsiveness, plant species were classified as non-mycotrophic, low, medium and high mycotrophic (Smith and Smith, 2013). Other variables, such AMF species and abiotic and biotic soil parameters, can also affect the AMF benefit to crops in term of biomass (Hoeksema et al., 2010; Lehmann et al., 2012; Suriyagoda et al., 2014). In addition, the diversity and composition of AMF communities varies widely in different climatic zones (Öpik et al., 2010). Since AMF species richness is positively related to plant productivity (van der Heijden et al., 1998), one can argue that climate can affect plant response to AMF. Indeed, climate modifies soil nutrient availability for plants and fungi leading to changes in their growth and likely influencing the outcome of symbiosis.

Wheat (*Triticum* spp.) is a major food crop, widely grown around the world under diverse climatic conditions (Marris, 2008) and classified as non-mycotrophic or mycotrophic according to the structure and composition of its genome (Hetrick et al., 1993). A total of 237 million ha of wheat was grown in 2012, yielding over 670 million t of grain (FAOSTAT, 2014). So far, the application of AMF as a sustainable management approach for field-grown wheat is not straightforward, due to the high variability of plant responses. Although many field studies have assessed the benefits on wheat due to indigenous, non-inoculated AMF and have addressed the possibility of increasing wheat nutrient uptake, growth and yield by AMF inoculation, a meta-analysis of how wheat field responses vary and depend on environmental and biological factors is lacking. Meta-analyses provide an objective and quantitative method to synthesize the results of different studies on a common scale including information on the sign and magnitude of an effect of interest from each study (Gurevitch and Hedges, 2001; Koricheva et al., 2013; Borenstein et al., 2014). In the present study we conducted a meta-analysis of published field trials aiming to answer to the following questions:

(1) Does field AMF inoculation increase wheat nutrient uptake, growth and grain yield?
(2) Is an increased mycorrhizal colonization due to AMF inoculation associated with changes in wheat nutrient uptake, growth and grain yield?
(3) Is an increased mycorrhizal colonization by non-inoculated AMF (indigenous) associated with changes in wheat nutrient uptake, growth and grain yield?
(4) Do soil texture, pH, organic matter (OM), total N, available P, AMF species and climate affect wheat response to inoculated and non-inoculated AMF in terms of wheat growth and grain yield?

2. Materials and methods

2.1. Literature survey and database construction

A database of effects of AMF on nutrient uptake, growth and grain yield of wheat was built by surveying peer-reviewed literature within the Web of Science Citation Index Expanded database (Thomson Reuters) and Scopus (Elsevier). The search, covering the period from January 1960 to June 2014, aimed to identify articles that reported effects of AMF on wheat growth in field conditions. The search phrases used were “mycorrhiza* AND triticum” and “mycorrhiza* AND wheat”, which yielded 326 and 874 publications in Web of Science, respectively, and 339 and 408 publications in Scopus, respectively. Articles were screened for studies performed under field conditions (Table 1; Fig. 1). Articles reporting experiments performed in controlled environments (greenhouse or climatic chamber) were excluded, as were those in field conditions in which fumigation or other soil sterilization methods were used, because they disrupt microbial processes. To be included in the database, articles needed to report data on nutrient uptake, growth or yield at maturity, a measure of the variance (standard deviation, standard error) or the statistical significance (t- or *P*-value), and the sample size.

To build a database for statistical analysis and hypotheses testing, the selected articles were split into three groups:

Group 1: wheat was inoculated with AMF and AMF root colonization rate was measured;
Group 2: wheat was inoculated with AMF, but AMF root colonization rate was not measured;
Group 3: wheat was not inoculated, but root colonization rate by non-inoculated AMF was measured.

To perform reliable bias tests, response variables were included if reported in at least three articles per group. The methods accepted for nutrient analysis in soil and plant tissues are given in Tables S1 and S2. Groups 1 and 2 included articles having non-inoculated plots (control) to distinguish between inoculated and non-inoculated plants. Data from soil AMF inoculation and seed coating were accepted.

For inclusion in groups 1 and 3, articles were screened for the characterization of AMF in soil and within host-plant roots by morphological and molecular tools. The articles included needed to report the method of staining and for assessing root AMF colonization at the stage of wheat maturity. Accepted methods for AMF colonization assessment are given in Table S3. Since molecular identification of AMF within roots was not performed in any article, the accepted molecular methods are not provided.

In addition, we accepted the following treatments for all three groups of articles: wheat genotype, location, year of cultivation, method of cultivation, tillage, mineral and organic fertilization, irrigation, preceding crop and chemical herbicides, insecticides and fungicides.

This final screening yielded 12, 10 and 16 articles for groups 1, 2 and 3, respectively. From each article, data for plant dry weight and tissue N, P and micronutrient concentrations and contents at maturity were extracted and entered into the database. In some cases, data were extracted by the Graph Grabber software package (Quintessa, 2009). We used nutrient concentration as a measure of tissue quality and nutrient content as an indication of crop agronomic performance. The following information was also extracted: (i) host species [i.e., *Triticum aestivum* L. and *Triticum turgidum* L. ssp. *durum* (Desf.) Husn.]; (ii) host variety or line; (iii) inoculated AMF species or isolate and technique of application; (iv) treatment (i.e., location, fertilization, year of cultivation); (iv) soil type (i.e., texture, pH, OM concentration); (v) geographic location (latitude, longitude and elevation); and (vi) N, P and K fertilization (rate and timing). For articles that included data from more than one treatment, the values from all treatments were included in the database if their independence was verified by a pseudoreplication test (Vilà et al., 2011).

2.2. Composition of the database

The database contains trials from India (11), North America (7) and China (5), which are the top three wheat producing regions in the world (over 55 million t per year) (Table 1; Fig. S1). In addition, five trials were carried out in Australia. Central Europe, with the highest yield per ha, is underrepresented, with four trials, as well as Africa, Central and South America and Japan with one trial each (Fig. 1). The Mediterranean region was not represented in the articles. Bread wheat was studied in most trials (314 out of 333), whereas durum wheat was studied only in two trials (Canada and India, 19 observations) (Table 1).