Applied Soil Ecology 112 (2017) 1–10

Contents lists available at ScienceDirect

Applied Soil Ecology

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

Species-specific responses to forest soil inoculum in planted trees in an abandoned agricultural field

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ARTICLE INFO

Article history:
Received 1 April 2016
Received in revised form 27 December 2016
Accepted 29 December 2016
Available online 6 January 2017

Keywords:
Abandoned agricultural field
Ecological restoration
Forest soil inoculation
Tree seedlings
Tree growth
Mycorrhizae

ABSTRACT

Tree plantations are commonly used to restore abandoned agricultural fields with varying degrees of success. Agricultural soils differ from forest soils in nutrient availability and microbial communities. The objective of this study was to test the effect of adding small amounts of forest soil on the survival, growth and rates of mycorrhizal fungal colonization of trees planted in an abandoned agricultural field over the crucial first three growing seasons. Seedlings of two arbuscular mycorrhizal (AM) and two ectomycorrhizal (EM) tree species were planted in an abandoned agricultural field. Soil inocula were taken from four forest stands, each dominated by one of the planted species. Half of the soil samples were sterilized before inoculation to distinguish microbial from nutrient effects. The effect of the quantity of soil inoculum added was tested using 300 and 1500 ml of forest soil. Tree mortality was low and did not vary between treatments. The growth of EM tree species responded, positively or negatively, to forest soil inoculation. A negative feedback was detected on the growth of red oak seedlings inoculated with red oak soil. Seedlings inoculated with EM sterilized soils were smaller than control seedlings, presumably due to lower nutrient availability of EM forest soils compared to agricultural field soil. The majority of the effects, either positive or negative, were observed the first year. After three seasons of growth, only yellow birch seedlings that had received 1500 ml of non-sterilized red oak soil still benefited from soil inoculation. More research is needed in nutrient-limited soils to determine whether inoculation would have greater or longer term benefits on tree survival and growth.

1. Introduction

Long-term intensive agricultural activities may decrease soil organic carbon, nutrient availability as well as microbial biomass (Dick, 1992; Lal, 2004; Rosenzweig et al., 2016). A reduction in mycorrhizal diversity and mycelium abundance has also been reported in such sites (Helgason et al., 1998; Alguacil et al., 2008). It has recently been suggested that soil microbial communities could be manipulated to enhance the success of ecological restoration (Heneghan et al., 2008; Harris, 2009; Hoeksema et al., 2010). Mycorrhizal fungal and bacterial inoculations have been previously tested to improve the survival and growth of outplanted nursery-produced tree seedlings (Trappe, 1977; Kropp and Langlois, 1990; Torrey, 1992). However, plant response (e.g. biomass) to inoculation could be greater if instead of using a single mycorrhizal fungus, several mycorrhizal fungal species and non-mycorrhizal microbes are present in the inoculum, or whole–community soil is used as an inoculum (Hoeksema et al., 2010; Urgiles et al., 2014). In effect, mycorrhizal function and behaviour are generally stimulated by an array of soil organisms, although some inhibitory interactions are possible (Fitter and Garbaye, 1994).

A simple method to inoculate trees would be to add soil containing desirable mycorrhizal fungal spores to a site that is deficient in these fungi (Schwartz et al., 2006), such as forest vs agricultural soils. Diversities of arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) fungi are higher in forest soils than in

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http://dx.doi.org/10.1016/j.apsoil.2016.12.008
0929-1393/

agricultural soils, but AM fungi are more abundant than EM fungi in agricultural soils (Helgason et al., 1998; Berman and Bledsoe, 1998; Dickie and Reich, 2005). Moreover, soils with high carbon levels and well-balanced nutrients generally have a positive impact on tree nutrition (Pinno et al., 2010; Ens et al., 2013). Therefore, adding a small amount of forest soil to an abandoned agricultural field could potentially create planting microsites that optimize tree survival and growth.

Most studies exploring the effects of forest soil inoculum on tree seedlings have used pot studies and/or have conducted short-term (<1 year) experiments (Packer and Clay, 2000; O'Brien et al., 2011; Urgiles et al., 2014; Dulmer et al., 2014). In pot studies, effects of forest soil transfer were observed on seedling growth, but the soil inoculum was mixed with a sterilized substrate (Borchers and Perry, 1990; O'Brien et al., 2011; Urgiles et al., 2014). Thus, tree seedlings had access to an environment in which the added microbes were not competing with field microbes. Previous field experiments using soil transfer to tree seedlings usually showed an increase in EM fungal colonization, but the presence or absence of effects on growth depended on soil provenance, field conditions, and tree species (Amaranthus and Perry, 1987; Helm and Carling, 1993; Berman and Bledsoe, 1998; Dickie et al., 2007).

The main objective of this study was to evaluate the effects of adding forest soil to tree seedlings planted in an abandoned agricultural field and to follow their survival and growth over three growing seasons. The specific objective was to compare the responses of two ectomycorhizal (EM) tree species and two arbuscular mycorrhizal (AM) tree species to different soil inoculation treatments. Since associations with EM fungi usually confer more benefits to tree seedlings than associations with AM fungi (van der Heijden and Horton, 2009; Bradford, 2014) and AM fungi should be more abundant than EM fungi in agricultural soils, a greater response from EM tree seedlings was expected. We also questioned the effect of host specificity and soil provenance: does soil inoculum collected under a mature tree of the same species have effects similar to that of inoculum collected under a different species on the receiving seedling? Since many mycorrhizal fungi are not host specific (van der Heijden and Horton, 2009), we hypothesised no effect of soil provenance.

2. Materials and methods

2.1. Study area

The experiment was conducted at the city of Montréal's tree nursery, in the suburb of L'Assomption (45°48′38″N; 73°26′26″W). The region is characterized by a humid continental climate. For the 1981–2010 period, the average annual temperature recorded at the nearest weather station (Verchères, 45°46′N; 73°22′W) is 6.6 °C, with monthly means of 21 °C in July and −10 °C in January while average annual precipitation is 984 mm, of which almost 20% falls as snow (Environment Canada, 2015). The experiment was established on two adjacent abandoned agricultural fields separated by a 5 m wide buffer of young Norway spruce (*Picea abies*). Soil is a fine to very fine sandy loam (IRDA, 2008). Fields were mown once or twice a year since the end of agricultural crop production more than 15 years ago. Mowing promoted ruderal herbaceous vegetation dominated by grass and clover species which are hosts of arbuscular mycorrhizal species.

2.2. Experimental design

This controlled field experiment began in May 2012 and the last growth measurements were taken at the end of the third growing season in August 2014. Four 12 × 36 m blocks were delineated in the largest abandoned field. Another block of the same size was delineated in the smallest abandoned field. Blocks were located at least 5 m away from a forested strip and more than 30 m from the road to avoid edge effects. Each block was divided into two sections: the first for AM tree species and the second for EM tree species. Two AM tree species, red ash (*Fraxinus pennsylvanica* Marshall) and red maple (*Acer rubrum* L.), and two EM tree species, yellow birch (*Betula alleghaniensis* Britton) and northern red oak (*Quercus rubra* L.), were planted. Each half block was divided into 9 plots using a random split-plot design. For the first half of each block, the treatments were: (1) soil quantities (0 ml, 300 ml or 1500 ml of loose soil); (2) soil sterilization (sterilized or not, hereinafter named live soil); (3) soil provenance (red ash or red maple forest soils) and (4) tree species (red ash or red maple) (Fig. 1a). For the other half of the blocks, the first two factors were the same, but the soil provenance and tree species treatments were replaced by the EM species yellow birch and red oak (Fig. 1b). In each plot, 3 seedlings of the same species (9 plots, 5 blocks, 4 species) were planted (total of 540 seedlings).

These four hardwood species were selected because they are native to the area and seedlings are readily available. All four species have intermediate shade tolerance (Niinemets and Valladares, 2006). Container-produced one year-old seedlings were provided by the Berthierville nursery of the Quebec Ministry of Forests, Wildlife and Parks. This nursery does not inoculate seedlings with any microbes. Once delivered, seedlings were kept in a dark room (4 °C, 90% humidity) before planting. Seedlings were manually planted at 2 m spacing on May 14 and 15, 2012 after the herbaceous vegetation was mowed.

Following planting, a white 50 × 50 cm polyester and polypropylene felt mulch (Arbo-Pro, Texel, Saint-Elzéar-de-Beauce, Canada) was placed around each tree seedling to reduce herb competition and maintain a stable climate while allowing water to penetrate the soil. In the rows between seedlings, vegetation was mowed every month during the summer. Each tree seedling was protected from small mammal predation using a plastic tree protector (Timm Enterprises Ltd, Milton, Canada). Tree protectors were 30 cm high for red ash, red maple and red oak seedlings, and 20 cm for the smaller yellow birch seedlings. No signs of herbivory were observed.

2.3. Soil collection and inoculation

Soils were collected in forest stands located within a 100 km radius of the study area between May 7 and 9, 2012. AM forest soil samples were collected in the forests in proximity to the island of Montréal, whereas EM forest soils were collected in the Lower Laurentians, starting about 60 km north of Montréal where the EM species are more abundant. More specifically, soil supporting red ash trees was collected in a woodlot outside the city of Laval, in an agricultural setting, approximately 35 km southwest of the study area (45°40′36″N; 73°43′39″W). The woodlot is composed of many broadleaf species, but the soil was taken in a section dominated by more than 70% mature red ash trees. The soil has a high activity of earthworms (A. St-Denis, pers. obs.) due to its neutral pH (calcareous glacial till). It developed into a Melanic Brunisol (Soil Classification Working Group, 1998) or Eutric Cambisol (IUSS Working Group WRB, 2015).

Soil supporting red maple trees was collected in a relatively pure red maple stand bordering a river, near the city of Boisbriand, located about 50 km southwest of the study area (45°35′52″N; 73°50′04″W). The soil developed from a fluvial deposit and transitions from Gleysols to Gray Brown Luvisol (or Albic Luvisol) (Soil Classification Working Group, 1998; IUSS Working Group WRB, 2015), depending on drainage. Soil has high P content due to previous agricultural land use on the uphill portion of the site.