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Do arbuscular mycorrhizal fungi play a role in the ability of rare plant species to colonize abandoned fields?

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Abstract

While some plant species colonize abandoned agricultural fields and dry grasslands with similar frequency (generalists), others are absent or underrepresented in abandoned fields (specialists). We tested if inoculation with dry grassland or abandoned field soil could improve specialist performance in an abandoned field and compared the effects of inoculation in the stage of sown seeds and transplanted seedlings. Arbuscular mycorrhizal fungi from abandoned field had higher root colonization potential. This could explain the higher performance of the sown specialists inoculated with the abandoned field inoculum compared to those inoculated with dry grassland inoculum. This difference disappeared when specialists were transplanted instead of sown. The results do not provide any support for higher performance of specialists inoculated with dry grassland inoculum. Transplantation, however, seems to be efficient way to introduce specialists into the abandoned fields.

Keywords

Abandoned fields; Arbuscular mycorrhizal fungi; Dry grasslands; Generalists; Mycorrhizal propagules; Revegetation; Specialists; Species diversity; Transplant experiment

1. Introduction

The economic changes in many areas of Central and Eastern Europe in the last 25 years have led to a strong increase in the number of abandoned agricultural fields (Knappová et al., 2012; Alcantara et al., 2013; Pereira and Navarro, 2015; Lasanta et al., 2017). These habitats are now undergoing natural secondary succession being colonized by species from surrounding habitats such as dry grasslands (Pereira and Navarro, 2015). However, some species cannot settle or are underrepresented in the abandoned fields (i.e. specialists) while others are present with similar frequencies in both abandoned fields and dry grasslands (i.e. generalists) (Münzbergová, 2004; Tremlová and Münzbergová, 2007; Knappová et al., 2012). As a result, plant communities in the abandoned fields have significantly lower species diversity than those in the dry grasslands (e.g., Kindscher and Tieszen, 1998; Knappová et al., 2012, 2013). Consequently, many projects try to modify the course of secondary succession by sowing or transplanting target species into the abandoned fields (Wallin et al., 2009; Török et al., 2011; Jongepierová and Prach, 2014). Although this management increases plant species diversity, its effectiveness is often questionable, as many of the reintroduced species are not able to establish viable populations in these sites in long-term (Bischoff et al., 2006; Foster et al., 2007; Török et al., 2011; Knappová et al., 2013).

The low performance of the specialists in the fields may be caused by changes in soil conditions due to previous agricultural practices. Long-term usage of fertilizers, pesticides and fungicides can have negative effects both on chemical and physical properties of the soil as well as on soil biota, including arbuscular mycorrhizal fungi (AMF) (Helgason et al., 1998; Oehl et al., 2004; Gryndler et al., 2006; Barber et al., 2013; Duchicela et al., 2013; Alguacil et al., 2014). AMF act as extensions of plant roots and increase plant nutrient uptake, especially of phosphorus (Smith and Read, 2010). AMF may also enhance plant resistance to pathogens (Pozo et al., 2010), play a key role in the plant community structure and increase plant

diversity (Francis and Read, 1994; van der Heijden et al., 1998; Dostálek et al., 2013; Köhl et al., 2014) by promoting establishment and abundance of subordinate species (Urcelay and Díaz, 2003; Lin et al., 2015; Bennett and Cahill, 2016).

Several studies trying to explain the inability of specialists to settle in abandoned fields focused on their interactions with the AMF. They demonstrated that the specialists are more AMF-dependent than the generalists (Urcelay and Diaz, 2003; Yao and Zhu, 2009). In line with this, Voříšková et al. (2016) demonstrated that dry grassland specialists are more colonized by AMF than generalists. Moreover, specialists and generalists may differ in the composition of their AMF communities. Specialists generally interact with more specific and less abundant AMF, while generalists interact with more ubiquitous and abundant AMF species (Öpik et al., 2006, 2009; Davison et al., 2011). Suppression of the AMF thus mainly affects the AMF taxa interacting with the specialists (Fry et al., 2017) leading to their loss from the community (Dostálek et al., 2013). The change at the level of AMF due to former agricultural management could, therefore, affect the capacity of specialists to settle in the abandoned fields.

Consequently, it can be predicted that the diversity of specialists in an abandoned field soil might be supported by inoculation of the abandoned field soil by soil communities from a dry grassland. This technique of vegetation restoration has been already successfully applied in diverse ecosystems (Huante et al., 2012; Middleton and Bever, 2012; Bauer et al., 2015; Wubs et al., 2016). However, its efficiency depends on the proximity between the donor and the receptor sites (Pywell et al., 2007; Kardol et al., 2009; Baasch et al., 2016; Fry et al., 2017; Pánková et al., 2018). In addition, the stage of plant development at which the inoculation with the targeted microbial community is performed may also impact the success of inoculation and subsequent plant establishment and performance (Verbruggen et al., 2013). Inoculation of seeds of the specialists with the target microbial community after sowing into

an abandoned field ensures that the plants experience the natural selection pressures at the localities, as these are likely the strongest at the initial stages of plant establishment. However, sowing could lead to competition with resident vegetation limiting the success of specialist establishment (Knappová and Münzbergová, 2015). Another restoration method is, therefore, to introduce the specialists by planting inoculated seedlings (Török et al., 2011). Pre-inoculation of the seedlings allows the microbial community to establish in plant roots before exposed to competition with faster growing soil biota and the seedlings to establish before being outcompeted by the surrounding vegetation (Mummey et al., 2009; Verbruggen et al., 2013).

In our study, we focused on the effect of soil microbial community on the establishment of specialists in an abandoned field located in the Czech Republic, Central Europe. The area is characterized by a mosaic of dry grasslands and neighbouring abandoned fields which were intensively cultivated until the end of 1980's (Chýlová and Münzbergová, 2008). Voříšková et al. (2016) who studied the AMF community composition of the dry grassland soil and the abandoned field soil that we used in our experiment noticed that the same AMF taxa were present in both sites, but their relative abundances were significantly different between the two sites. In addition, the abandoned field AMF communities were characterized by lower number of propagules, but faster plant root colonization (Knappová et al., 2016; Voříšková et al., 2016). Thus, they could negatively affect the slow-growing specialists but could be more efficient for the fast-growing generalists (Jansa et al., 2008; Fry et al., 2017). We aimed to study the importance of soil microbial community for the ability of specialists to settle in the abandoned fields and assess if the stage of plant development, i.e. seed or seedling, at which the plant was inoculated and introduced to the site, could affect the results. Among the microbial community, we focused on the AMF as we assumed that AMF are the most important part of the soil community for growth of the specialists (Maltz and

Treseder, 2015). We asked the following questions: (i) Does inoculation by the dry grassland soil support growth of specialists in the abandoned field?, (ii) Do AMF from the dry grassland and the abandoned field differ in their ability to colonize roots of specialists? and (iii) Does the effect of inoculation by the dry grassland soil differ depending on plant age?

2. Materials and methods

2.1. Study site

Our study was conducted on two sites situated on a marl soil (Studnička, 1972), a calcareous dry grassland and a directly neighbouring abandoned field, located in northern Bohemia (50° 30' 2.627" N, 14° 18' 57.45" E), Czech Republic (Supplementary data 1). Based on our previous studies, this site was selected to represent a typical locality of the České středohoří region (Chýlová and Münzbergová, 2008). The species-rich semi-natural dry grassland was only grazed and mown in the past and hosts vegetation of the *Bromion* community (Ellenberg, 1988). Agricultural management of the field, through monocultures, fertilizing and tillage, ended approximately 25 yr ago. The abandoned field is progressively colonized by the dry grassland species with a lower diversity than the dry grassland, lacking many grassland specialists (Knappová et al., 2012). Voříšková et al. (2016) demonstrated that the abandoned field used in our study has higher pH, P and K contents but lower total N and C, Mg, organic C and carbonate contents than the dry grassland (Supplementary data 2).

2.2. Species selection

Ten plant species were selected (Table 1) among different plant families to cover a large spectrum of species from the studied sites. The plant species differed in their dependence on AMF (see Voříšková et al., 2016 for some species) and in frequency of their occurrence in grasslands and abandoned fields (Knappová et al., 2012). The species were

selected to form pairs of phylogenetically related species, i.e. belonging to the same plant family, to eliminate differences given by distinct phylogenetic histories. Each pair was made by the two plant types, i.e. one species growing only in the dry grasslands or underrepresented in the abandoned fields (referred to as specialist) and one species growing with similar frequency in both the dry grasslands and the abandoned fields (referred to as generalist) (Münzbergová, 2004; Tremlová and Münzbergová, 2007; Knappová et al., 2012). To obtain a large amount of seeds for all the selected species and to avoid the use of seeds from the same area that could induce potential bias in the plant growth due to the co-evolutionary history between the soil and the plants, the seeds were purchased from a local seed producer, Planta Naturalis, Markvartice (<http://www.plantanaturalis.com>). These seeds came from natural sites from the same area (up to 100 km from the study region) and had been cultivated under standardized conditions of the seed provider for less than 3 generations.

Table 1 Plant species selected for both the sowing and the transplant experiments.

Plant species	ID Pair	Plant type ¹	Family
<i>Sanguisorba minor</i>	A	S	Rosaceae
<i>Agrimonia eupatoria</i>	A	G	
<i>Briza media</i>	B	S	Poaceae
<i>Brachypodium pinnatum</i>	B	G	
<i>Centaurea scabiosa</i>	C	S	Asteraceae
<i>Centaurea jacea</i>	C	G	
<i>Aster amellus</i>	D	S	Asteraceae
<i>Inula salicina</i>	D	G	
<i>Linum tenuifolium</i>	E	S	Linaceae
<i>Linum catharticum</i>	E	G	

¹ (G) Generalist, (S) Specialist

2.3. Sowing experiment

Permanent plots of 0.3×0.3 m were set up on the abandoned field along three transects (Supplementary data 3a). The permanent plots were disturbed by digging to a depth of approximately 0.3 m to remove all the vegetation including roots before the experiment. We did this since our previous studies indicated that disturbance may facilitate growth and flowering of plants in the abandoned fields (Knappová et al., 2013). The permanent plots were grouped by four, inside each transect, to form a set of two crossed treatments, i.e. sowing and inoculation treatments. The sowing treatment contained plots with sown seeds and control plots without seed addition. The inoculation treatment contained plots inoculated with non-sterile soil from the dry grassland and the control plots, i.e. plots inoculated with non-sterile soil from the abandoned field. Thus, we had four treatments: inoculated with dry grassland soil + seeds, inoculated with abandoned field soil + seeds, inoculated with dry grassland soil + no seeds and inoculated with abandoned field soil + no seeds. The inoculation was realized by taking non-sterile soil from the dry grassland or from the abandoned field, and by distributing it on the soil surface of the plot in a layer of 1 cm. Each treatment was replicated three times, i.e. once in each transect, resulting in a total of 12 plots (3 transects \times 2 sowing treatments \times 2 inoculation treatments, Supplementary data 3a). In October 2012, seeds of all the selected plant species (Table 1) were sown into the plots to fulfil stratification demands of the individual plant species. The number of seeds used per plot was determined as the amount of seeds produced by each plant species per 1 m^2 (Tremlová and Münzbergová, 2007). The number thus varied between species and reflected natural seed production of the species. All the species were sown together in the same plots.

In June 2013, the established seedlings in the plots were recorded and marked with colour pins. During four subsequent plot inspections (July and September 2013 and 2014), we recorded survival of marked seedlings and searched for newly emerged ones to obtain the

total number of germinated seedlings. Non-target species were removed from the plots at each inspection. For each of the five inspections we also evaluated the plant size for each seedling by multiplying the plant height and the number of leaves. For pairs B and E (Table 1), the plant size corresponded to the plant height because the number of leaves cannot be properly measured for such species.

2.4. Transplant experiment

The transplant experiment was established in March 2013 with all 10 species (Table 1). The seeds of all the species were germinated in sterilized sand for one month to obtain seedlings that we could handle without damaging the most fragile species. In April 2013, the one-month seedlings were transferred into $5 \times 5 \times 5$ cm pots containing a mixture of sterilized sand, sterilized nutrient-poor soil and dry grassland or abandoned field inoculum in 1:1:1 ratio. The sterilization was made by γ -irradiation at 25kGy. The nutrient-poor soil was a marl soil from another site than the two biotopes studied to avoid biases due to co-evolutionary history between the plants and the soil. This soil served as a substrate for plant establishment and the poor nutrient content favoured the establishment of symbiotic interactions. The inoculum was prepared by sampling $10 \times 10 \times 10$ cm soil samples from 10 sites (5 m apart) along transects across each biotope. For each biotope, the 10 samples were mixed and homogenised to obtain one soil sample representative of the dry grassland and one soil sample representative of the abandoned field. Then, the soils were sieved through 4 mm sieve and the plant roots were cut into small pieces before returning back to the soil. We used this inoculated soil mixture instead of direct plant cultivation in the dry grassland or abandoned field soil to provide the same starting conditions for all the species. There were 35 replicates of each treatment (dry grassland vs. abandoned field inoculum) per species, i.e. 70 individuals

per species in total. The seedlings were cultivated for two months in a greenhouse with 25°C day temperature, 10°C night temperature and 14-h photoperiod.

In May 2013, the plant size was measured for each seedling as described in the sowing experiment. The success of the AMF root colonization resulting from the inoculation was checked microscopically, at 100× magnification, on five individuals per species after 0.05% Trypan blue staining of one third of the central part of the root system (Koske and Gemma, 1989). As all plants were successfully colonized, the remaining seedlings were randomly transplanted 20 cm apart from each other in several segments along five transects in the same abandoned field as the sowing experiment (see Supplementary data 3b for the experimental layout). The transects were 2 m apart. The different species and inoculation treatments were fully intermixed within each segment where all the species and treatments were replicated. Vegetation around each transplanted plant was clipped in a circle of a diameter of 20 cm to facilitate successful plant establishment. The plant size and survival of transplants were recorded five times during our study, in June, July and September 2013 and in June and September 2014.

At harvest, in October 2014, the plants were dug out and transferred to the laboratory. Then, shoots were cut, and roots were washed. To detect a potential role of AMF in the plant resistance to fungal endophytes, the abundance of endophytic fungi in the roots was estimated under a compound microscope at 200× magnification and ranged along a scale of abundance, where 0 corresponded to their absence, 1 to very low occurrence, 2 to presence of several fungal endophytes and 3 to roots highly colonized by fungal endophytes. Endophytic fungi were defined as all the fungi present in the roots that were not AMF and could potentially negatively affect the host plant. A part of fine roots, representing about one third from the central part of the root system, was stained in 0.05% Trypan Blue in lactoglycerol (Koske and Gemma, 1989). The frequency of AMF root colonization was evaluated according to Trouvelot et al. (1986) on

30 segments with a compound light microscope at 200× magnification. The shoots were dried at 70°C for 72 h to evaluate the aboveground dry biomass.

2.5. Estimating mycorrhizal inoculation potential in the soils

The soil mycorrhizal inoculation potential (MIP), i.e. the potential that AMF propagules present in the soil establish mycorrhizal colonization in the roots of the host plant, was estimated in May 2013 on both biotopes. To estimate MIP, we used a standard bioassay approach with maize (a universal AMF host) as a host plant (Wilson and Trinick, 1983). The same two soil samples, representative of each biotope, as those used to prepare the inocula in the transplant experiment (see above) were diluted with γ -sterilized soil taken from the studied biotope in a ratio of 1:100 (v:v). The prepared substrates were filled into 125 ml pots. One pre-germinated maize seed (*Zea mays* L. cv. TATO) was planted into each pot. Five replicates were used for each substrate. The plants were cultivated in a greenhouse for 6 weeks. At harvest, the plants were excavated from the soil. The roots were washed and stained in 0.05% Trypan Blue (Koske and Gemma, 1989). MIP was estimated as the percentage of the root length of the host plant colonized by AMF. Colonization was assessed using a gridline-intersect method on 200 intersects per sample (Giovannetti and Mosse, 1980) under a dissecting microscope at 40× magnification.

2.6. Data analyses

For both the sowing and the transplant experiments, plant size and survival which followed normal and binomial distribution, respectively, were tested with repeated measurement analyses due to the dependency between dates of measurement using generalized linear mixed effect models (Buckley et al., 2003; Bolker et al., 2009; Bates et al., 2014). This allowed testing of the effects of time and interactions between independent

variables and time. In addition, at each date of measurement, the significance of the effect of independent variables on plant size and survival was tested separately by generalized linear model (GLM).

For the sowing experiment, inoculum (from abandoned field or dry grassland), plant type (specialists or generalists) and their interaction were used as predictors. Transect was used as a covariate to account for possible spatial heterogeneity of the experimental area. Due to the different success of establishment of the species in the field, data were missing for several species. It was thus not possible to test the effect of species pair as a predictor. To take into account the species pair in our analyses, we therefore standardized plant size for each species pair. We considered the 95 % quantile of the plant size of each pair from the transplant experiment (as we had sufficient data for all the species only in the transplant experiment) as 100 % and expressed the individual plant size relative to this value. This was done because each pair was composed by two phylogenetically related species having a similar body constitution. Such a method allows a better comparison between all the species. We took the 95 % quantile to avoid using the maximal plant size that could represent an outlier.

For the transplant experiment, inoculum (from abandoned field or dry grassland), plant type (specialists or generalists), species pair (Table 1) and their interactions were used as predictors. Transect, position on transect and transect \times position on transect, representing the distances of the planted plants from the edge of the experimental area, were used as covariates to account for possible spatial heterogeneity of the experimental area (Supplementary data 4, 6-7).

Concerning the final measurements, for the sowing experiment, we tested the number of seedlings by GLM with normal distribution. This final time of measurement, i.e., September 2014, was the most representative of the number of seedlings. The number of

seedlings in the sown plots was calculated for each of the three transects by subtracting the number of seedlings in the control plots. The same independent variables as described above for the sowing experiment, i.e., the predictors and covariate, were used. For the transplant experiment, at the final time, i.e., October 2014, GLM with normal distribution were used to test aboveground biomass, fungal endophyte abundance and AMF root colonization. The same independent variables as described above for the transplant experiment, i.e., the predictors and covariates, were used (Supplementary data 5-7).

To test the relationship between the plant parameters of transplant (plant size, survival, aboveground biomass and fungal endophyte abundance) and the AMF root colonization, the same GLM (with normal or binomial distribution) were performed by adding AMF root colonization and its interactions with inoculum, plant type and species pair as predictors. The MIP was compared between the two soils with t-test.

To improve the normality of the residuals, plant size was log transformed, aboveground biomass was square root transformed and AMF root colonization was arcsin transformed. Normality and variance equality of the dependent continuous variables were tested by Shapiro-Wilk and Bartlett tests, respectively. The statistical analyses were performed using the statistical software JMP 7 (SAS Institute, Cary, NC) and R version 3.3.2 (R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria) with an alpha level of 0.05.

3. Results

3.1. Effect of inoculation soil origin on performance of plants established from sowing and transplant experiment in the abandoned field

Plant size of the sown species was affected by the inoculum \times plant type interaction (Table 2). Thus, with the dry grassland inoculum, generalists were larger than specialists,

while the situation was reversed with the abandoned field inoculum (Fig. 1A). The transplants were larger with the abandoned field inoculum than with the dry grassland inoculum (Table 2, Fig. 1B). Whatever the plant stage at which the inoculation was performed, plant size was affected by plant type (Table 2). For sown species, generalist plants were bigger than specialists (Fig. 1A) while for transplants the situation was reversed (Fig. 1B). The survival of both the sown species and the transplants was significantly affected by inoculum origin and plant type (Table 2). Thus, the plants inoculated with the abandoned field inoculum and the specialists survived more than plants with the dry grassland inoculum and generalists (Fig. 1C, D).

Plant size and survival for both the sown species and the transplants were affected by the interactions between the predictors and the time (Table 2). For the sown species, the specialists tended to be larger with the abandoned field inoculum than with the dry grassland inoculum which disappeared with time, while it was the opposite for the generalists (Fig. 1A). For the transplants, the positive effect of the inoculum from abandoned field on plant size, as compared to the inoculum from dry grassland, faded with time for the specialists (Fig. 1B). In addition, with time, the generalists tended to be larger with the abandoned field inoculum than with the dry grassland inoculum. Finally, for the sown species, the higher survival of specialists than generalists with the abandoned field inoculum disappeared with the dry grassland inoculum (Fig. 1C). For the transplants, however, the effects of inoculum and plant type on the survival remained unchanged over time (Fig. 1D).

The plant traits measured to represent the final performance of plants established from sowing and transplant experiments were the number of established seedlings and the aboveground biomass, respectively. The number of seedlings was significantly affected by the inoculum \times plant type interaction (GLM: $\chi^2 = 6.54$, $P = 0.011$). The specialists tended to establish more seedlings than generalists with the abandoned field inoculum while this

difference faded with the dry grassland inoculum (Fig. 2A). The aboveground biomass of transplants was higher for specialists than generalists (Table 3, Fig. 2B).

Table 2 Generalized linear mixed effect models explaining plant size and survival over time in the sowing and the transplant experiment. For the sowing experiment, inoculum, plant type and their interaction were used as predictors and transect was used as covariate. For the transplant experiment, species pair, plant type, inoculum and their interactions were used as predictors, and transect, position on transect and their interaction were used as covariates (Supplementary data 4). Values in bold are significant at $P \leq 0.05$.

	Sowing experiment					Transplant experiment				
	Plant size			Survival		Plant size		Survival		
	<i>df</i>	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>	
Inoculum	1	2.11	0.147	7.84	0.005	16.90	<0.001	25.68	<0.001	
Plant type	1	6.05	0.014	4.39	0.036	18.71	<0.001	31.73	<0.001	
Inoculum \times Plant type	1	4.04	0.044	1.76	0.185	1.37	0.242	1.11	0.292	
Time	1	3.98	0.046	4.01	0.045	6.19	0.013	7.44	0.006	
Time \times Inoculum	2	11.27	0.004	10.02	0.007	6.27	0.044	7.46	0.024	
Time \times Plant type	2	11.26	0.004	4.01	0.134	12.32	0.002	7.44	0.024	
Time \times Inoculum \times Plant type	4	15.53	0.004	10.19	0.037	12.57	0.014	7.46	0.114	

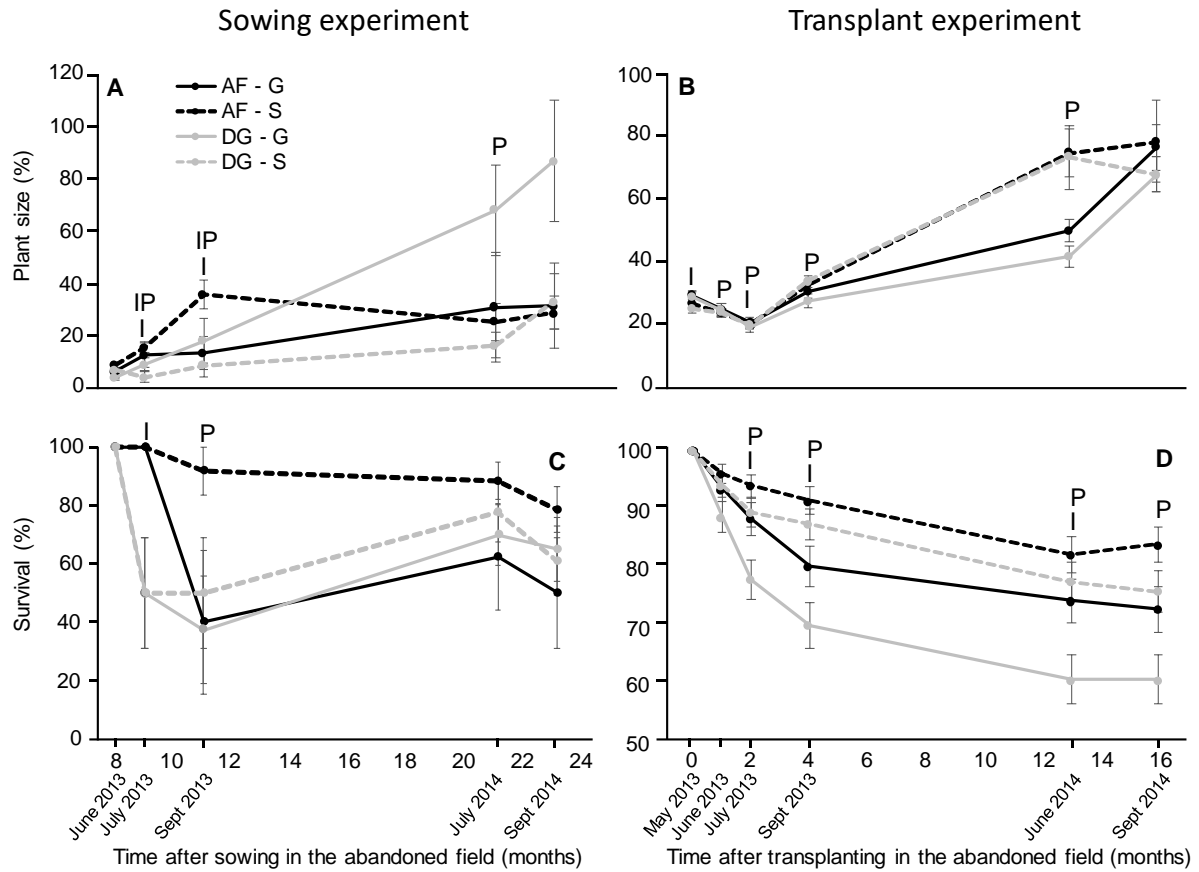


Figure 1 Effect of inoculum origin (from AF: abandoned field or DG: dry grassland) and plant type (G: generalists or S: specialists) on plant size and survival over time, in the sowing experiment (A, C) and in the transplant experiment (B, D). The x-axis indicates the number of months after sowing or transplanting the plants in the abandoned field, and the dates indicate the times of measurements. Error bars represent the standard errors of the mean. For the sowing experiment, both the tests and graphics used the standardized plant size while for the transplant experiment, the plant size was standardized for the graphic only. The plant size was standardized by species pair (Table 1), i.e. by considering the 95 % quantile of the plant size within each pair from the transplant experiment as 100 % and reporting the individual plant size relative to this value. I, P and IP indicate a significant effect of inoculum, plant type and inoculum × plant type, respectively, after generalized linear models performed for each time separately ($P \leq 0.05$).

3.2. Fungal characteristics and their implications for transplant performance in the abandoned field

At the beginning of the transplant experiment, in May 2013, there was a significantly higher MIP of the abandoned field soil (mean \pm SE: 46.3 ± 1.2 %) compared to the dry grassland soil (mean \pm SE: 23.9 ± 4.4 %) ($t = -4.84$, $P < 0.001$).

At harvest, AMF root colonization was not affected by inoculum origin or plant type (Table 3). Moreover, AMF root colonization was not related to any of the plant performance parameters nor to the fungal endophyte abundance ($P > 0.06$ in all cases).

Abundance of fungal endophytes was not affected by inoculum origin or plant type (Table 3).

Table 3 Generalized linear models explaining the plant and fungal parameters in the transplant experiment, at harvest, in October 2014. Inoculum, plant type, species pair and their interactions were used as predictors. Transect, position on transect and their interaction were used as covariates. See Supplementary data 5 for details of the test with all predictors and covariates. Values in bold are significant at $P \leq 0.05$.

	Aboveground biomass			Fungal endophyte abundance		AMF root colonization	
	<i>df</i>	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>
Inoculum	1	0.42	0.52	0.69	0.41	0.99	0.32
Plant type	1	17.71	<0.001	1.79	0.18	0.02	0.89
Inoculum \times Plant type	1	0.35	0.56	0.05	0.82	0.91	0.34

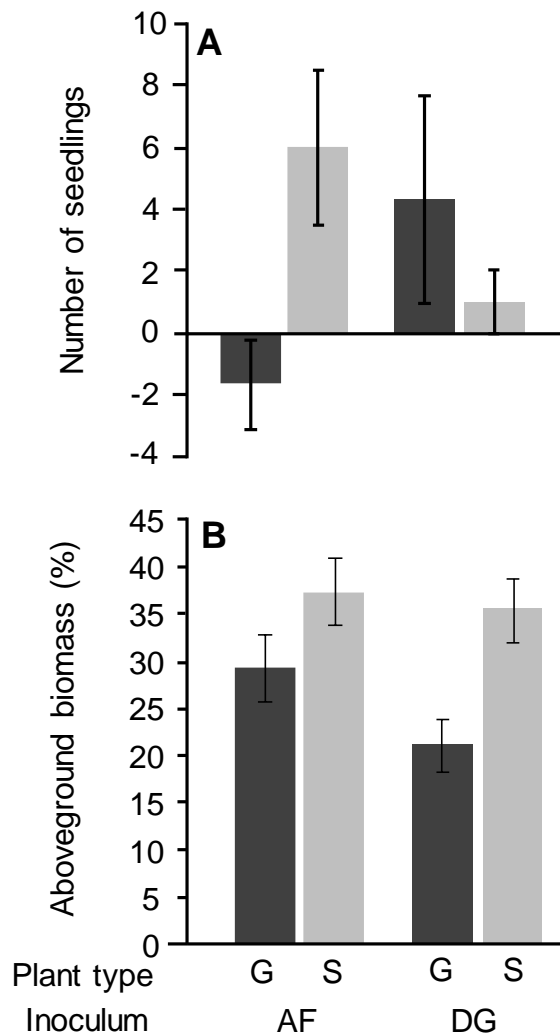


Figure 2 Effect of inoculum origin (from AF: abandoned field or DG: dry grassland) and plant type (G: generalists or S: specialists) on (A) number of seedlings in the sowing experiment and (B) aboveground biomass in the transplant experiment. Error bars represent the standard errors of the mean. For graphic representation, the aboveground biomass was standardized by species pair (Table 1), i.e. by considering the 95 % quantile of the plant size within each pair from the transplant experiment as 100 % and reporting the individual plant size relative to this value.

4. Discussion

4.1. Effect of inoculation soil origin on performance of plants established from sowing and transplant experiment in the abandoned field

Contrary to what we expected, in the abandoned field soil, the performance of specialists was better with the abandoned field inoculum than with dry grassland inoculum. This effect of inoculum was more pronounced in the sowing than in the transplant experiment. This poor performance with the dry grassland inoculum suggests that the microbial community was not adapted to the abandoned field soil conditions. This maladaptation can be caused by both abiotic and biotic properties of the abandoned field soil. Among abiotic limitations, the chemical and physical properties of the abandoned field may be important. AMF are adapted to their soil (Pánková et al., 2011, 2014) and the functioning of plant-AMF interactions is strongly dependent on the soil nutrient content (Hart and Reader, 2002; Johnson et al., 2003; Lin et al., 2015). The former agricultural practices enrich the soil with nutrients (Lavelle et al., 2005; Isbell et al., 2013; Tilman et al., 2014), and our abandoned field soil was enriched in phosphorus (Voříšková et al., 2016). Consequently, as the plants acquire enough phosphorus via the root pathway, their interaction with the symbiotic fungi may become costly, limiting plant growth (Johnson, 1993; Barber et al., 2013; Johnson and Graham, 2013). This may be more important with the dry grassland AMF because they are costlier for the host plant than the abandoned field AMF. Indeed, it was previously demonstrated that the dry grassland AMF communities contain more sporocarpic species (Oehl et al., 2010) and produce more arbuscules than the abandoned field AMF (Oehl et al., 2004). This has also been demonstrated by Pánková et al. (2018) for the dry grassland AMF community used in the present study. Such internal fungal structures are highly costly for the plant (Feddermann et al., 2010).

Concerning the physical properties of the abandoned field soil, agricultural practices usually decrease the soil aggregate stability and the soil organic matter content (Mårtensson and Olsson, 2012; Duchicela et al., 2013). Indeed, the abandoned field soil used in this study was poorer in organic carbon than the dry grassland soil (Voříšková et al., 2016). In addition,

the soil was disturbed at the beginning of the experiment to increase subsequent plant performance (Knappová et al., 2013). Numerous studies have demonstrated that the abandoned field AMF communities are composed of ubiquitous AMF taxa able to colonize a large range of habitats including those highly disturbed (Oehl et al., 2003, 2010; Sýkorová et al., 2007). The soil disturbances could thus negatively affect establishment of the dry grassland AMF but allow the abandoned field AMF to rapidly colonize the soil and the plants. This may explain why the dry grassland inoculum was less efficient toward the host plants.

Among the biotic causes that could limit the efficiency of the dry grassland inoculum, Sýkorová et al. (2007) demonstrated that the ubiquitous AMF taxa, like those present in abandoned fields, are more competitive for nutrients than the more specific AMF taxa, i.e. those present in the dry grasslands. Thus, we may suppose that, in the abandoned field soil, the less competitive dry grassland AMF community had to compete with the native AMF community of the abandoned field. This could decrease or inhibit the positive effect of the dry grassland inoculum on plant performance. We could also hypothesise that the microbial community from the abandoned field may negatively affect the dry grassland AMF and its interaction with the plants. Indeed, Revillini et al. (2016) demonstrated that local bacteria adapted to AMF promoted AMF growth and its efficiency toward the host plant performance. For example, invasive species may disturb the performance of native species by modifying the local soil microbial community which affects the endophyte symbionts interacting with the native species (Rudgers and Orr, 2009).

The fact that the beneficial effect of the abandoned field inoculum on the specialist performance compared to the dry grassland inoculum tended to disappear in the transplant experiment is in accordance with our initial hypothesis. Indeed, we may suppose that pre-inoculated seedlings allowed the dry grassland AMF to properly colonize the plants, limiting competition with the abandoned field AMF as well as the potential disruption caused by the

abandoned field soil microbial community. These results suggest that the stage at which the inoculation was performed had an impact on the specialist establishment in the abandoned field. This could confirm the expectation that seedling pre-inoculation allows AMF to better colonize and adapt to the host plant and thus to be more efficient (Mummey et al., 2009; Verbruggen et al., 2013). In addition, over time, the plant performance was better for specialists than generalists in the transplant experiment only. This was in accordance with the fact that the AMF community, whatever its origin, seemed more efficient when inoculated at the seedling stage than at the seed stage.

4.2. Fungal characteristics and their implications for transplant performance in the abandoned field

A significantly higher MIP was found in the abandoned field soil than in the dry grassland soil. This is in agreement with previous studies (Barni and Siniscalco, 2000; Richter et al., 2002; Martinez and Johnson, 2010; Voříšková et al., 2016). This could be explained by a change in the abundance of the different AMF propagules, i.e. spores, external hyphal attached to the roots, hyphal fragments and infected root fragments (Richter et al., 2002), reflected by a change in the composition of the AMF communities due to former agricultural practices (Hart and Reader, 2002; Voříšková et al., 2016). The mechanical and chemical disturbances tend to select AMF taxa producing more spores (van der Heyde et al., 2017) and infecting the host plants by spores and hyphal fragments (Richter et al., 2002; Martinez and Johnson, 2010). Indeed, such soil management practices negatively affect the external hyphal network attached to the plant and progressively decrease the abundance of AMF taxa producing such external structures (Gryndler et al., 2006; van der Heyde et al., 2017). As a result, the more competitive AMF selected in the abandoned field soil are those producing

spores (López-García et al., 2014; van der Heyde et al., 2017) which could explain the higher soil MIP value recorded.

Higher MIP might be correlated with a better ability of AMF propagules present in the soil to initiate mycorrhizal colonization of plant roots, reflecting a higher abundance of infective propagules. However, we did not observe any difference in AMF root colonization between plants inoculated with the abandoned field inoculum compared to the dry grassland inoculum. Richter et al. (2002) made the same observation by measuring the MIP and the root colonization in an abandoned field and an adjacent dry grassland in Arizona, USA. Thus, the MIP might not be a good predictor of the abundance of AMF propagules (Martinez and Johnson 2010; Voříšková et al. 2016). Voříšková et al. (2016) found, by focusing on the same sites as we did, higher MIP in the abandoned field soil accompanied by a significantly lower number of infective propagules compared to the dry grassland soil. They suggested that the AMF from abandoned field are fast plant colonizers which compensated for the lack of infective propagules. As a result, they colonized the roots rapidly at the detriment of the dry grassland AMF. MIP may thus not reflect the potential of the soil fungal propagules to colonize plant roots.

The fact that we found no relationship between plant parameters and AMF root colonization suggests that the effect of the inoculum origin on plant performance is not due to the level of root colonization. This is in accordance with the hypothesis of a difference in the speed of root colonization previously mentioned (Voříšková et al., 2016). However, we cannot exclude the effect of the rest of the microbial community. The whole community has a fundamental role in the positive effect of the AMF on the host plant (Frey-Klett et al., 2007; Paluch et al., 2013; Emam, 2016; Wubs et al., 2016). The hypothesis of maladaptation of the dry grassland AMF to the abandoned field soil could be the same for the rest of the microbial community (Bever et al., 2010; Middleton and Bever, 2012). However, Rúa et al. (2016)

demonstrated a minor role of the rest of the soil microbes in their meta-analysis of the compatibility between plant, soil and AMF.

The introduction of specialists into the abandoned field soil should, therefore, include an intervention to change the soil properties prior to modifications of AMF and associated microbial community. Indeed, concerning the soil, the aim is to suppress the negative effects of former agricultural practices on the soil abiotic properties. Some studies tested the effect of top-soil removal demonstrating a beneficial effect on the plant and soil composition in an abandoned field soil after inoculation by grassland soil community (Klimkowska et al., 2007; Török et al., 2011; Olsson and Ödman, 2014; Wubs et al., 2016). Concerning the possible interventions on the AMF community composition, the inoculation of specific AMF taxa adapted to the soil conditions and efficient toward the target species could be a solution (van der Heijden, 2004; Vogelsang et al., 2006). Moreover, as the rest of the microbial community is also important, it is necessary to understand the functional role of these microbes toward the plant/AMF relationship. Indeed, Requena et al. (2001) found that co-inoculation of AMF with a nitrogen-fixing rhizobacteria enhanced the establishment of subordinate species on desertified ecosystems. Finally, the transplant method seemed to be a better way to inoculate plants than the sowing method.

4.3. Conclusions

The effects of inoculum origin and plant type on plant performance demonstrated that, in our study, the cultivation of specialists with the dry grassland inoculum did not support their growth in the abandoned field. However, the abandoned field inoculum played an important role for seedling establishment and plant performance over time. The abandoned field soil properties could partly explain the absence of positive plant response to the dry grassland inoculum. The inability of the specialists to settle in the abandoned field soil after

inoculation with the dry grassland inoculum seems to be mainly due to soil chemistry and the mal-adaptation of the AMF community to this soil. It seems, therefore, necessary to act at the level of soil, to mitigate the effects of former agricultural practices on soil properties, and at the level of microbial community, specifically AMF, to find the AMF adapted to the soil conditions and efficient toward the target species. Such a management could improve the success of re-introduction of specialist plant species in abandoned fields. Moreover, inoculation of the seedlings seems to be more efficient for the subsequent specialist performance than inoculation of the seeds.

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