The potential of soil inoculation in terms of seedling establishment and growth for restoration projects

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Directory

1 Abstract

Restoration aims to return degraded areas into a state with improved ecosystem functioning and is highly important regarding the fact that 50-75% of all terrestrial ecosystems are modified due to anthropogenic activities. Multiple studies highlight that restoration projects should take into account the soil microbiome because especially mycorrhizal fungi can strongly enhance the establishment and growth of plants. In literature there are examples which showed beneficial as well as detrimental impacts of soil inoculation. This study reviews the impact of soil inoculation on plant growth responses and presents factors and mechanisms which contribute to enhanced or reduced plant growth when inoculation is applied. Data was collected from 44 different studies specifically for the response variables plant height, survival and biomass. The log response ratio is calculated for each experimental unit in order to combine data for treatments (soil inoculation) and controls. Overall, plants treated with mycorrhizal inoculum showed significantly higher growth responses compared to controls. No significant difference in terms of the type of study (field or lab conditions) was detected even though lab studies were found to result in higher plant growth responses in previous meta-analyses. There was also no significant difference on plant growth responses regarding the soil origin of the inoculum (conspecific or heterospecific). The outcome of inoculation seems to be complex as many factors are at play as for example the land use history at the field site or the amount and diversity of fungal propagules in the applied inoculum. In conclusion, soil inoculation is a promising approach and can complement well established restoration techniques but the outcome will depend on the used plant species, the features of the inoculum and the local circumstances.

2 Introduction

Symbiotic associations between plant roots and fungi are called mycorrhiza (Dighton 2009). Mycorrhizal fungi provide limiting nutrients as phosphorus or nitrogen as well as water to their symbiotic plants and can enhance their resistance to biotic and abiotic factors (Chandra et al. 2010, Soudzilovskaia et al. 2019, Vahter et al. 2020). These factors include greater resistance to drought or heavy metals (abiotic) and protection against pathogens or grazing invertebrates (biotic) (Vahter et al. 2020). Additional benefits are increased soil aggregate stability what may reduce erosion (Emam 2015). Overall, mycorrhizal symbiosis leads to a higher seedling establishment, survival, growth and greater competitive ability compared to other seedlings (Ramos-Zapata et al. 2006). The plant community structure is also affected by mycorrhizae as not all plants have the same dependency or capacity to form mycorrhizal associations (Dighton 2009). In return, plants provide carbohydrates to the fungi (Dighton 2009).

One can distinguish between different dominant forms of mycorrhiza: In endomycorrhizae the fungus penetrates the epidermal wall of the plant. This type encompasses arbuscular as well as ericoid mycorrhiza. In the other large group, the ectomycorrhizae, a significant part of the fungal biomass is outside the plant root. Interestingly, ectomycorrhizal hyphae can extend considerable distances what increases the access area of plants for nutrients and water to a high degree (Dighton 2009). Over 85% of the vascular plants in terrestrial biomes form mycorrhizal symbioses and only a minority is not interrelated with mycorrhizal fungi (Dighton 2009, Soudzilovskaia et al. 2019). Ecosystem functioning therefore strongly depends on the presence of mycorrhiza. Arbuscular mycorrhiza is the predominant type in grasslands (Vahter et al. 2020, Koziol et al. 2021). The same is true for tropical rain forests (Urgiles et al. 2009). Ectomycorrhizal symbioses are mainly found in trees in temperate and boreal ecosystems (Frey-Klett et al. 2007, Grove et al. 2019).

50-75% of the terrestrial ecosystems are modified due to anthropogenic activities what illustrates the far reaching impact humans have on ecosystems and their functioning (Soudzilovskaia et al. 2019). The high deforestation rate in the tropical forests threatens biodiversity, increases carbon losses and alters the hydrological regime in those areas (Urgiles et al. 2009). In 2020 the loss if primary tropical forest increased by 12% in 2020 from 2019. This means more than 10 million acres were lost in 2020 (The New York Times 2021). Other typical human impacts with negative consequences for ecosystems are livestock rearing, forest burning, mining, logging or heavy metal contamination which lead to forest degradation via soil compaction, loss of soil moisture or changes in the structural complexity of nearby forests (Soteras et al. 2013, Policelli et al. 2020). The mentioned disturbances also affect the soil microbiome and mycorrhizal fungi in terms of abundance and diversity (Williams et al. 2011, Huante et al. 2012). Similar trends are observed in grasslands, ecosystems with a high biodiversity and large losses of natural area. Typical drivers in these ecosystems are land-use intensification and nitrogen deposition. Maintaining grassland ecosystems is difficult due to conflicting economic interests but crucial to maintain the high biodiversity. Next to conservation, restoration of abandoned agricultural land, urban brown fields or post mining landscapes can be taken into account (Vahter et al. 2020).
For restoration it's important to foster an initial species composition and to ensure the survival and establishment of the community in degraded ecosystems. Depending on the degree of disturbance different targets can be reached. Restoring an ecosystem back to its pre-disturbance status is called true restoration whereas rehabilitation means restoration to an intermediate successional state. If the ecosystem is irreversibly changed due to severe

disturbance, a completely new community can be obtained. This restoration process is called reclamation (Asmelash et al. 2016).

Restoration projects in any degraded locations promote ecosystem services and bring broad benefits. These encompass ecological, economic and social benefits. As an example, restoration of native vegetation reduces carbon losses and therefore avoids further emissions of greenhouse gases into the atmosphere (Soudzilovskaia et al. 2019). Or successful forest plantation techniques can help to achieve high yields of wood which can be used as a sustainable resource. A typical example would be plantations of *Acacia mangium* in Malaysia (Jeyanny et al. 2011).

There are many common restoration techniques as top soil removal, seeding, hay transfer or mowing (Cole 2007, Carbajo et al. 2011). Re-establishing the native microbiome in areas with anthropogenic pressure is still rarely considered in restoration projects. However, there is growing realization that the soil microbiome contributes to successful restoration and that projects neglecting the soil microbiome often fail (Koziol et al. 2021). The soil biota is sensitive to altered soil conditions due to agricultural processes, crop monocultures or the application of fertilizers (Koziol et al. 2021). Also after clear cuts and burning, the organic matter content in the soil is often reduced and there are shifts in the soil microbial community and a reduced number of viable seeds and fungal propagules (Amaranthus and Perry 1987, Korb et al. 2004). Given this sensitivity and the importance of soil microbes for plant establishment, it is crucial to consider these symbionts in restorations of degraded areas.

The questions addressed in this study are: a) Does soil inoculation promote plant establishment and growth responses? and b) Which further factors influence the response to soil inoculation?

In literature one can find many parameters related to mycorrhizal fungi itself as mycorrhizal abundance, diversity or colonization. However, the focus of this study is clearly on variables related to the plant establishment and growth. Multiple different inoculation techniques are considered as whole soil inoculation, soil transplantation (transfer of larger amounts of soil), inoculation with roots or extracted fungal communities from soil. Not considered are inoculation experiments with single fungal strains or the application of commercial inoculum.

Due to the known benefits that mycorrhizal fungi provide to their associated plants it is expected that inoculation of seedlings will increase plant establishment and growth responses.

3 Methods

Literature search and dataset construction

Systematic searching in Web of Science was done with the goal to get representative data of available experiments. Key words were *mycorrhiz**, *seedling* and different expressions for soil inoculation (soil inocul*, whole soil inocul*, soil transplant*, whole community inocul*) in order to reach a large range of inoculation experiments. Additionally, the references of useful papers in terms of data availability were screened. Studies must have met the following criteria in order to be included. First, only studies were taken into account which presented raw data for any of the investigated response variables (Table 1). Secondly, studies which used single fungal strains for inoculation or commercial inoculum were not considered. And thirdly, the study must consist of at least one treatment (inoculation with living organisms) and a corresponding control for which either sterilized field soil was added or no addition at all.

The collected variables with a short description are listed in Table 1. On the one hand, raw data for different response variables was collected which include plant height, plant biomass, seedling survival, plant cover as well as plant species richness and Shannon diversity as two biodiversity metrics. For each value of a specific response variable the error inclusive type of error and the sample size were recorded. If the data was presented in graphics, the tool GraphClick was used for precise data extraction.

On the other hand, independent variables were recorded (Table 1). Outcomes for the treatment and control were recorded in separate rows but the information that they belong together was kept. Ecosystems are often dominated by a specific type of mycorrhizal fungi, either by arbuscular (AM) or ectomycorrhizal (EM) fungi. If the information about the "dominant fungal type" was not directly extractable from the respective paper, the maps published by Soudzilovskaia et al. (2019) were used as a backup for the classification. Some plant species are known to form associations with both mentioned types of mycorrhizal fungi for which reason a third level called "mixed" was introduced (Cortese and Bunn 2017). For the variable "soil origin of the inoculum" it was just distinguished between two levels, either conspecific or heterospecific. The term conspecific was used if it's known that the inoculum originates from an area where the focal plant species is present, regardless of its abundance.

Table 1: Overview of response and independent variables collected for this study with a short description and a note if the data was used in the final analysis (AM: arbuscular mycorrhizae, EM: ectomycorrhizae).

Variables	Description	Analysis
Response variables		
Plant height (cm)	--	yes
Plant biomass (g)	Inclusive a note if values represent total, aboveground or belowground biomass	yes
Plant survival %	--	yes
Plant cover %	--	no
Species richness	--	no
Shannon diversity	--	no
Independent variables		
Study area	Coordinates of the study	no
Vegetation type	Forest and grassland as the major types, others (e.g. wetland, dryland, shrubland) were pooled	yes
Climate zone	Tropical, temperate, boreal	yes
Dominant fungal type	AM, EM, mixed	no
Type of study	Field, lab (greenhouse, mesocosm)	yes
Previous land use for field studies	Description as precise as possible according to the available information	no
Plant species	--	no
Treatment	Inoculation or no inoculation (controls)	yes
Soil origin of the inoculum	Conspecific, heterospecific	yes
time	Time between the onset of the experiment and data collection	no

Calculation of effect sizes and statistical analysis

To address the first research question, if soil inoculation promotes plant establishment and growth responses, the log response ratio was calculated as an effect-size index. The log response ratio is calculated as $L = \ln(\bar{X}_E / \bar{X}_C) = \ln(\bar{X}_E) - \ln(\bar{X}_C)$ and is useful to combine values for a specific treatment and its control. $\bar{X}_E$ and $\bar{X}_C$ stand for the mean outcome of an experimental and control group, respectively. Specifically, the investigated variables are plant height, survival and total biomass and data for each response variable was treated separately. In summary, a single log response ratio is calculated for each experimental comparison of a treatment group (inoculation) and its control (no inoculation). Furthermore, the analysis requires the standard deviations (SD_E, SD_C) and the sample sizes (n_E, n_C) of the experimental group and the control. Further information about the analysis can be found in the paper by Hedges et al. (1999).

The final goal was to calculate the weighted mean log response ratio $\bar{L}^*$ as well as its confidence interval. Positive values for $\bar{L}^*$ indicate that the experimental group (inoculation) has higher values in terms of plant establishment or plant growth compared to the controls, so an overall beneficial effect is visible. Negative values indicate the opposite. The weighting is only possible if a measure of error for each single experiment is known. As the error is not always extractable from the involved papers an additional, simplified analysis was performed by calculating the unweighted mean log response ratio $\bar{L}$.

For the second research question, mixed effects models were constructed using the R package "lmerTest" (R Core Team 2022). The different studies were modeled as random effects whereas other variables listed in Table 1 were included as fixed effects. The fulfillment of the model assumptions was checked and data transformation was not necessary. Model construction was strongly guided by the availability of data.

As an extension of the second research question, literature was screened for variables with an influence on plant growth responses if inoculation techniques are applied. This qualitative extension should complement the quantitative analysis and give a broader perspective on the success of inoculation experiments and the final restoration success.

4 Results

The weighted mean log response ratio $\bar{L}^*$ of the response variables height, survival and total biomass are all positive (Figure 1). Estimates are listed in Table 2. Confidence intervals of all pictured log response ratios only span over positive values, meaning soil inoculation leads to significantly higher values of a response variable compared to controls without inoculation. The analysis was repeated for the unweighted mean log response ratio $\bar{L}$ for which additional samples without known error could be included. However, this had no effect on the significance of the results. The corresponding figure can be seen in the Appendix.

For the response variable height, 87.4% of the single experiments (pair of treatment and control) report a positive log response ratio, meaning a benefit associated with soil inoculation. For the response variables survival and total biomass the values are 71.2% and 78.1%, respectively. These values are based on the whole available data (regardless of missing errors).

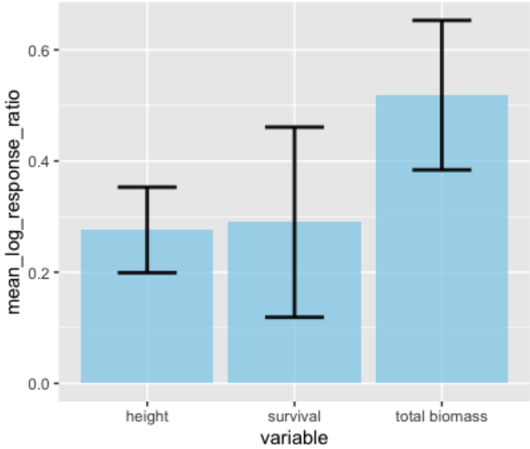

Figure 1: Weighted mean log response ratio of the response variables height, survival and total biomass. Error bars represent 95% confidence intervals.

Table 2: Estimates and numbers concerning the weighted mean log response ratio for the response variables height, survival and total biomass.

	Plant height	Survival	Total biomass
Weighted mean log response ratio $\bar{L}^*$	0.276	0.290	0.519
Standard error SE($\bar{L}^*$)	0.0394	0.0873	0.0688
95% Confidence interval	[0.199, 0.353]	[0.119, 0.461]	[0.384, 0.653]
Number of single log response ratios L	39	23	65
Number of studies	9	4	7

The following part is mainly restricted on the influence of explanatory variables on the log response ratios L for height due to limited data availability.

Figure 2 shows the distribution of the single log response ratios L for height for all included studies. Modelling the study (15 different studies) as a random effect, reveals that 52.8% of the total variance of the log response ratio for height is attributed to the effect of the study.

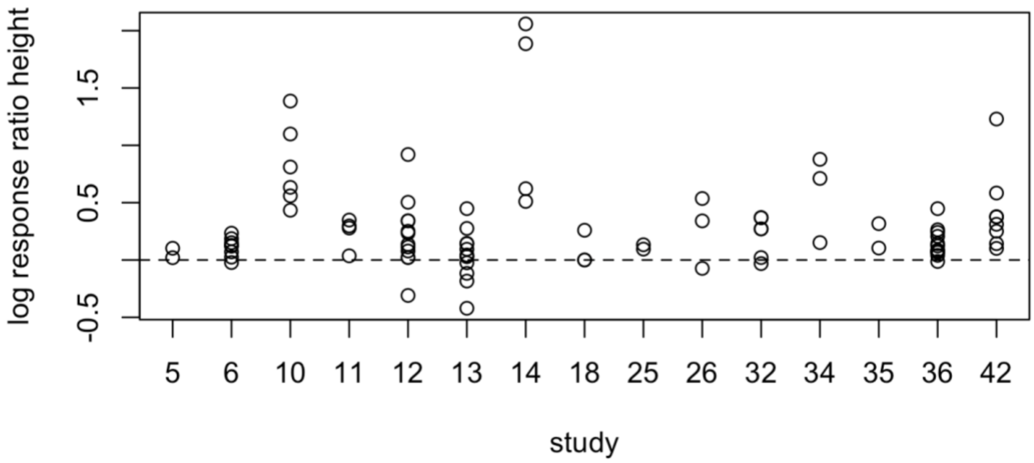

Figure 2: Single log response ratios (response variable height) for 15 different studies. The dashed line at a log response ratio of 0 represents the boundary for positive effects of inoculation.

As shown in Figure 3, growth responses in terms of plant height tended to be larger if the experiment was conducted under laboratory conditions (e.g. greenhouse) compared to field conditions. However, this difference turned out to be not significant ($p = 0.863$). Similar results were obtained when looking at the difference of conspecific and heterospecific soil inoculum. Conspecific inoculum led to slightly higher growth responses but there is no significance ($p = 0.501$). No difference was observed for inoculation experiments in the temperate and tropical climate zone ($p = 0.873$).

Data for total biomass could not be analyzed for differences in field and lab studies because all collected studies were by chance conducted in the lab. For the soil origin, the unequal proportions of the levels lead to unmeaningful results. However, this data set was more suitable to analyze differences concerning the climate zone and the vegetation type (Figure 4). Studies in tropical regions showed significantly higher growth responses in terms of total biomass compared to studies in temperate regions ($p = 0.0298$). Experiments in forest ecosystems show higher growth responses but this result is not significant ($p = 0.257$).

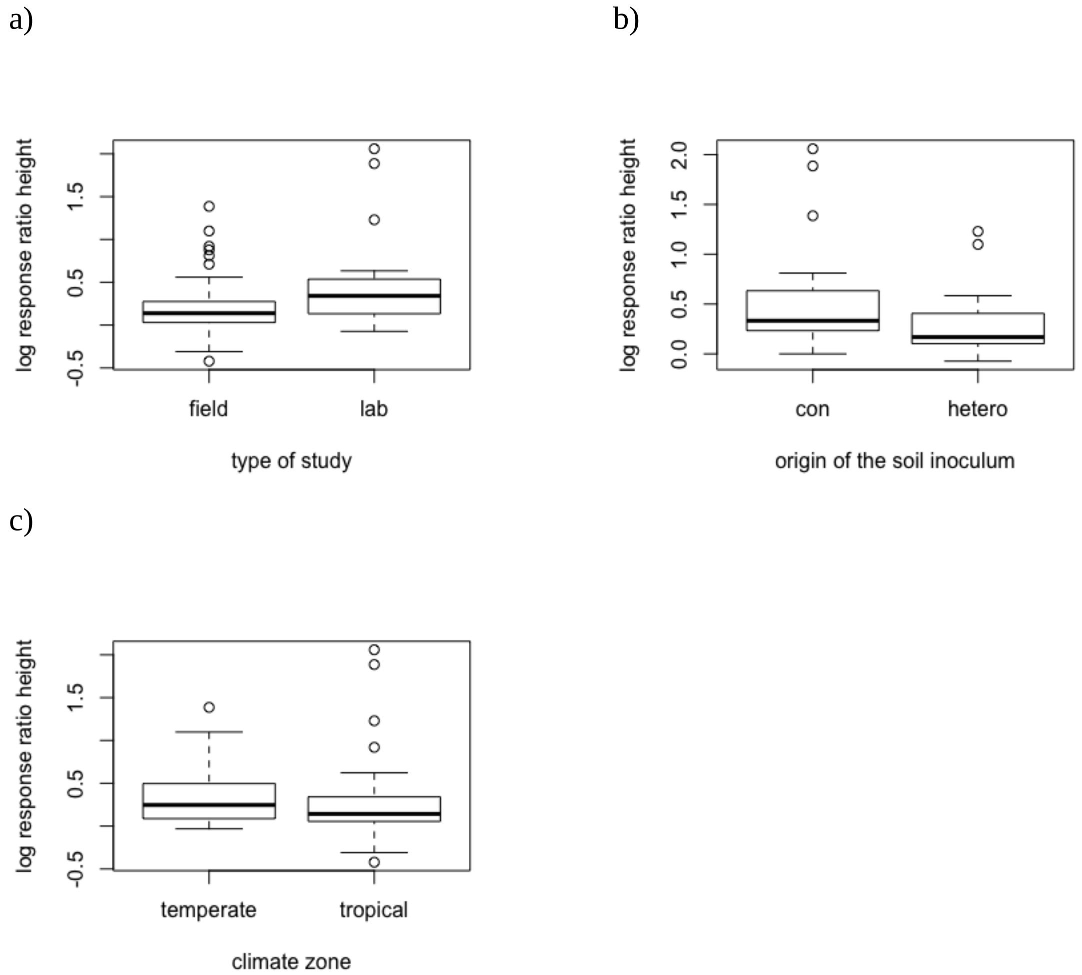

Figure 3: log response ratios of the variable height for a) field and lab studies (n_{total} = 87 from 15 different studies, n_{field} = 62, n_{lab} = 25), b) different origins of the inoculum (n_{total} = 38 from 9 different studies, n_{con} = 18, n_{hetero} = 20) and c) different climate zones (n_{total} = 87 from 15 different studies, $n_{temperate}$ = 28, $n_{tropical}$ = 59). There are no collected studies which measured growth responses in terms of height in boreal ecosystems.

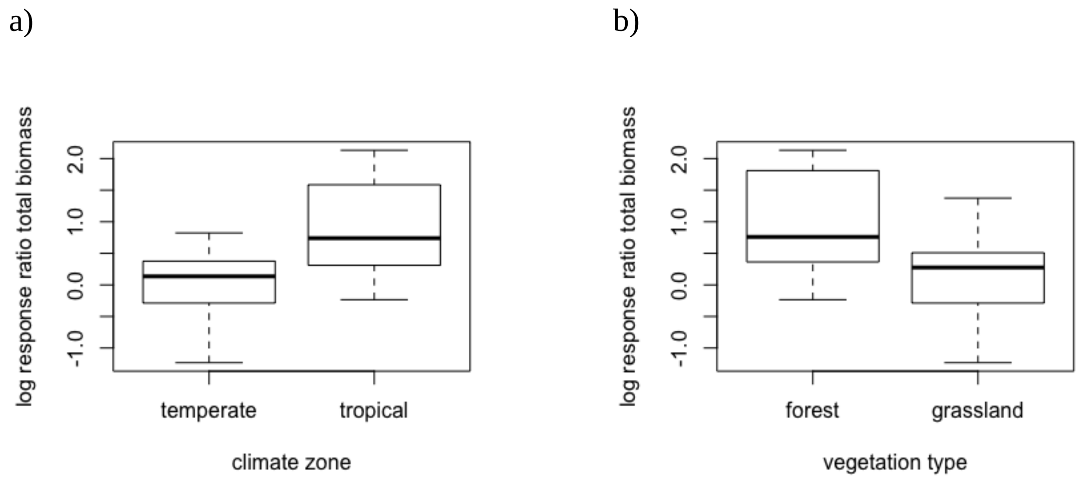

Figure 4: log response ratios of the variable total biomass for a) different climate zones (n_{total} = 70 from 8 different studies, $n_{temperate}$ = 30, $n_{tropical}$ = 40) and b) different vegetation types (n_{total} = 65 from 7 different studies, n_{forest} = 35, $n_{grassland}$ = 30). There are no collected studies which measured growth responses in terms of total biomass in boreal ecosystems.

There seems to be a lot of complexity concerning the outcome of plant growth if soil inoculation is applied. Figure 5 and the following paragraphs give an overview on potentially relevant impact factors.

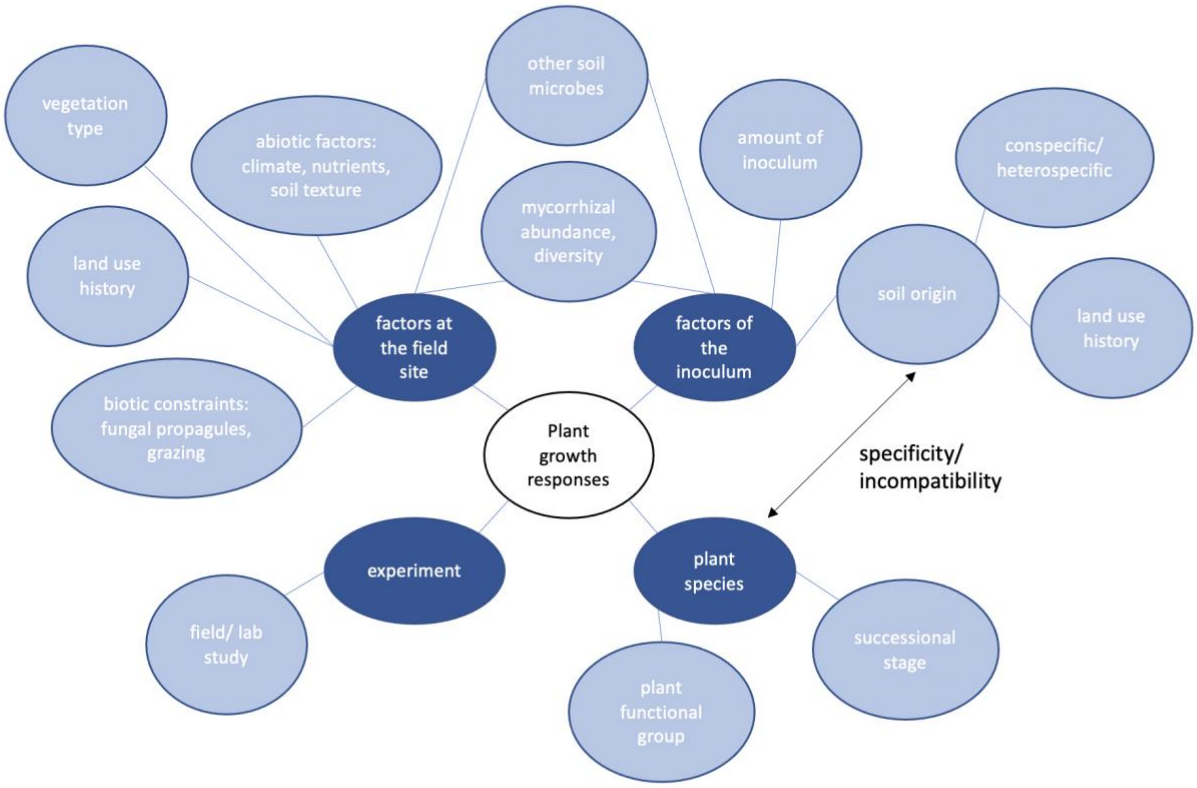

Figure 5: Overview on influencing factors on plant growth responses when inoculation is applied. Factors are associated with one of the four levels of the field site, inoculum, used plant species and experimental features.

There are many factors immediately at the restoration site (in the case of field studies) which are of consequence. Climate plays an important role, for example the impact of summer drought. In areas with such conditions early mycorrhizal formation is crucial and can be facilitated via inoculation techniques (Amaranthus and Perry 1987). Too harsh and dry conditions may be a limiting factor to develop functional mycorrhizal associations in a study by Gavito et al. (2008). Soil texture at the field site is relevant for the water holding capacity of soils and therefore influences the water availability to organisms (Amaranthus and Perry 1987). Further abiotic constraints are eutrophication and acidification of soils what can limit the success of restoration programs. That's why top soil removal is applied in some of the restoration projects with the goal to reduce the high soil fertility (Wubs et al. 2016). From the biotic perspective, limited seed availability at restoration sites, the soil community composition and the amount of fungal propagules can represent constraints (Wubs et al. 2016). Herbivory is another factor which was shown to limit seedling growth in the field (Michelsen 1993, Allen et al. 2005). Also land use activities change environmental factors at the site. Agriculture can decrease the level of organic carbon, change the nutrient availability and the microbial biomass (St-Denis et al. 2017). Slash pile burning was found to significantly alter soil properties and strongly reduces the number of viable seeds or fungal propagules. Soil compaction associated with the use of heavy mechanized equipment is another detrimental factor (Korb et al. 2004). Other examples which lead to severe soil degradation are mining activities for coal or copper. In such sites unassisted recover of soil microbiota as mycorrhizal fungi is difficult (Emam 2015).

Additionally to soil properties at the field site, soil properties of the inoculum matter. The amount of nutrients and organic compounds, soil moisture, pH and non-mycorrhizal biota influence the mycorrhizal formation (Amaranthus and Perry 1987). There can be differences in the inoculum potential in terms of the quantity and quality of fungal propagules (O'Brien et al. 2011). Moreover, individual mycorrhizal fungus species can exert a spectrum of effects on the plant host species depending on the specific species interactions (Kiers et al. 2000). So depending on the used plant species and fungal composition of the inoculum, outcomes of inoculation experiments are expected to vary. Furthermore, there is some evidence that higher plant growth responses are achieved by using a higher volume of inoculum (Carbajo et al. 2011, St-Denis et al. 2017). When working with whole soil inoculation, the applied soil may not only contain mycorrhizal fungi but also other soil microbes. It was shown than *Rhizobium spp.* enhances spore germination, mycelial growth and root colonization of arbuscular mycorrhizal fungi what indirectly also benefits the plant species (Barroetavena et al. 1998). Another example is the bacterial genus *Frankia*, which directly form a symbiosis with plants and provide assimilated atmospheric nitrogen (Urgiles et al. 2014).

At the level of the used plant species for restoration the dependency on mycorrhizal fungi should be noted. Mycorrhizal symbioses are formed in 85% of all plant species. The remaining species are non-mycorrhizal and are therefore not expected to benefit from mycorrhizal inoculation (Dighton 2009). Multiple studies report a stronger effect of inoculation for late-successional compared to early-successional plant species (Rowe et al. 2007, Carbajo et al. 2011, Koziol et al. 2021). This observation can be explained by the short term costs which arise when investing into mutualism and which are more severe for early-successional plants (Middleton et al. 2015). Also the plant functional group is an important explanatory variable for plant growth responses. It has been found that C4 grasses and woody plants without N-fixing symbionts responded stronger to inoculation than C3 grasses and plants with N-fixing symbionts, respectively (Hoeksema et al. 2010).

5 Discussion

A significant positive effect of soil inoculation was found when considering different response variables (plant height, survival, total biomass). This result is consistent with findings by Hoeksema et al. (2010). They found that individual studies ranged from positive to negative outcomes in terms of plant growth responses to inoculation but the weighted mean effect over all investigated studies was positive. Another meta-analysis by Piñeiro et al. also shows positive mean effect sizes for survival and plant height (2013).

Despite this overall positive effect, Figure 2 depicts that there are some examples with a detrimental effect of soil inoculation. It's known that interactions between plants and mycorrhizal fungi also depend on the environmental conditions. If environmental conditions are unsuitable, the mutualistic relationship can turn into a parasitic relationship (Rowe et al. 2007). Furthermore, inoculation could introduce pathogens. These facts explain to some extent why negative effects of soil inoculation can occur. For practice this implies that for an individual case plant growth responses to inoculation are hard to predict.

As presented in the results, the study matters regarding inoculation outcomes. It's obvious that conditions for different restoration projects are never identical. Interestingly, even at the same field site with the same plant species and origin of the inoculum, plant growth responses can differ one year later. For a specific study, this discrepancy was attributed to differences in the organic matter of the inoculum, the degree of herbivory and the outbreak of a fungal root pathogen (Allen et al. 2005).

Even though no effect of the experimental site (field vs. lab) was found, a meta-analysis by Lekberg and Koide shows higher growth responses to inoculation for plants grown in the glasshouse compared to field-grown plants (2005). Reasons could be environmental stressors as drought, predation or competition which are not apparent in controlled laboratory conditions. This implies that one should act with caution when extrapolating results under laboratory conditions to the field (Lekberg et al. 2005, Soteras et al. 2014).

The origin of the soil in terms of conspecific or heterospecific has no significant effect on the plant growth response. This could be explained by a trade-off for conspecific soil addition. Conspecific soil can on the one hand lead to greater growth responses as the mycorrhizal fungi are adapted to the specific plant species under investigation (O'Brien et al. 2011). However, there is no complete agreement on the degree of specificity for plant-fungal interactions. Some studies mention a specific compatibility between plant hosts and fungi (Kiers et al. 2000, Uibopuu et al. 2009) whereas other studies state that there is little specificity regarding interactions between plants and mycorrhizal fungi (Smith et al. 2011, St-Denis et al. 2017). On the other hand, conspecific soil is more likely to carry plant specific pathogens which negatively affect plant growth and survival. Such a mechanism was found in a study by Packer and Clay (2000) where seedling survival was greatly reduced when soil near to this specific plant species was used as inoculum. These findings are in line with the Janzen-Connell hypothesis which states that species coexistence is promoted by negative effects of soil pathogens (Packer and Clay 2000). To sum up, there can be circumstances in which the positive or negative effects of conspecific soil addition dominate. Another point concerning the investigated influence of conspecific vs. heterospecific soil is the broad classification with only two levels. But more precise classification is hard as the information about the soil origin or the abundance of the focal plant at the site where the inoculum comes from is often missing.

Regarding the effect of the climate zone, results are inconsistent. Whereas there is a significant difference in terms of total biomass, this difference is not visible for plant height. In literature, no information was found about the effect of the climate zone on the success of inoculation experiments. Moreover, one can't exclude the presence of indirect forces which lead to this significant result. This finding needs further verification with more studies.

An important constraint especially for the second research question is the limited data availability. Maybe the power to detect significant differences was too low with the available amount of data. Another issue is missing information. A combination of multiple explanatory variables as fixed effects in the mixed effects model would have further reduced the amount of data for which reason the models were kept simple. This means that the obtained results must be interpreted with caution as they only present the isolated effect of explanatory variables on response variables.

It would be interesting to investigate further influencing factors on plant growth responses to inoculation in a quantitative way (see Figure 5). Especially the level of degradation at the field site as well as at the site where the inoculum originates could be of relevance as mycorrhizal communities strongly respond to land use changes or degradation (Middleton and Bever 2012). For this analysis precise criteria for the level of degradation must be defined. In general, for the analysis of influencing factors, different levels of these factors should be equally represented in order to enable a comparison. That would be for example important for the factor "dominant fungal type" because collected data from study systems with ectomycorrhiza are underrepresented compared to arbuscular fungi.

Even if the overall effect of mycorrhizal inoculation on plant establishment and growth responses is positive, this can't directly be equalized with the main target, namely successful restoration. Many studies did short term experiments with a duration of less than one year. So the interpretation of the study results are limited to this early stages of seedling establishment. Nevertheless, the early stage is the critical phase for plant establishment and therefore important to reach successful restoration (Ramos-Zapata et al. 2006, Piñeiro et al. 2013). Moreover, inoculation may promote invasive species at the filed site what should be avoided (Emam 2015).

For practice, there are many more factors which are of importance. Restoration programs should not only focus on the inoculation itself but also manage habitat conditions at the field site if necessary (Vahter et al. 2020). For example if excessive soil fertility at the restoration site is an issue, top soil removal can improve habitat conditions (Carbajo et al. 2011). Additionally it's useful to assess the availability of fungal propagules at the site as well as in the soil inoculum. If the field site harbors a high mycorrhizal diversity and abundance, inoculation may be ineffective (Barroetavena et al. 1998, Emam 2015). The approach of soil inoculation should furthermore be realizable under sustainable conditions. Specifically, natural ecosystems which act as sources for the soil inoculum should not be disturbed what raises the question of large-scale application. It's important to keep the amount of inoculum as low as possible and simultaneously reach a high effectiveness. A study by Middleton and Bever presents evidence that restoration can impact many more plants in the surrounding than just the inoculated seedlings itself (2012). This finding is highly relevant for the realization of restoration projects with soil inoculation. To conclude, soil inoculation is a promising approach for restoration projects but the effectiveness of a specific soil inoculum can't be generalized and must be tested for a specific plant species and under the prevalent conditions.

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8 Appendix

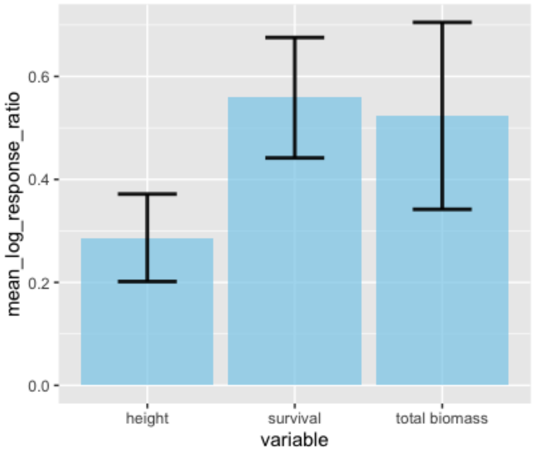

Figure 6: Unweighted mean log response ratio of the response variables height (n=87 from 15 studies), survival (n= 52 from 13 studies) and total biomass (n=70 from 8 studies). Error bars represent 95% confidence intervals.