Plant-soil feedbacks in boreal tree species

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Master's Thesis • 30 credits
Swedish University of Agricultural Sciences, SLU
Department of Forest Ecology and Management
Master's Program in Forest Ecology and Sustainable Management
Master thesis / Examensarbeten, 2023:18 • ISSN 1654-1898
Umeå 2023

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Credits:	30 credits
Level:	A2E
Course title:	Master's thesis in Forest Science - Forest Ecology and Management
Course code:	EX0958
Programme/education:	Master's Program in Forest Ecology and Sustainable Management
Course coordinating dept:	Department of Forest Ecology and Management
Place of publication:	Umeå, Sweden
Year of publication:	2023
Copyright:	All featured images are used with permission from the copyright owner.
Title of series:	Examensarbeten / SLU, Institutionen för skogens ekologi och skötsel
Part number:	2023:18
ISSN:	1654-1898
Keywords:	plant-soil feedback, plant economic spectrum, biotic and abiotic factors, sterilization-inoculation experiment, conspecifics and heterospecifics

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Abstract

Plant-soil feedback (PSF) is important for understanding how plants influence the composition and abundance of soil biota and nutrients and how this affects plant growth. The plant economic spectrum (PES) also plays a role. This study is a two-stage experiment that aims to determine the roles of plant traits and biotic and abiotic soil properties on PSF. Soil was collected from two sites in Sweden consisting of replicated monocultures of different tree species. Soil in each plot is considered to be "trained" by the planted species. A glasshouse experiment was set up with a live and sterilization-inoculation experiment using four boreal tree species (*Betula pendula, Picea abies, Pinus contorta,* and *Pinus sylvestris*). In the live experiment, seedlings were planted on live soil from each species and in the sterilization-inoculation experiment each species was planted on combinations of sterile soil and live soil inoculum. Biomass was taken and used to calculate PSF for each species. In the live experiment, *B. pendula* had significantly higher biomass than the other species which follows the predictions made based off the PES. *P. contorta* had positive PSF, although not significantly different, and the other species had negative PSF which was unexpected as it was predicted that all species would exhibit negative PSF. In the sterilization-inoculation experiment, soil inocula did not have a significant effect on PSF but some species had a significant species-soil origin interaction. This rejected the third hypothesis as it was predicted that soil inocula would follow the same patterns as the first experiment. This research has implications for the forestry industry as it can inform better on tree species choice and more sustainable forestry practices.

Keywords: plant-soil feedback, plant economic spectrum, biotic feedback, abiotic feedback, sterilization-inoculation experiment, conspecifics and heterospecifics

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Abbreviations

AM	Arbuscular mycorrhizal fungi
EcM	Ectomycorrhizal fungi
BP	*Betula pendula*
PA	*Picea abies*
PC	*Pinus contorta*
PES	Plant Economic Spectrum
PS	*Pinus sylvestris*
PSF	Plant-soil Feedback
SLU	Swedish University of Agricultural Sciences

1. Introduction

Boreal tree species have different growth strategies that range from slow to fast on the plant economics spectrum, on the one hand with fast-growing birch (*Betula sp.*) to on the other hand slow-growing Norway Spruce (*Picea abies*) (Li et al., 2021). Growth strategies are important for understanding the genetically determined rate at which various species allocate biomass under similar environmental conditions. However, it is not fully understood under which conditions plant growth strategies overrule the effects of other factors such as effects of microorganisms and soil nutrients. Early successional and deciduous species are generally fast-growing while coniferous species are generally slow-growing. This is due to fast-growing trees' greater ability to "do it itself." Therefore, a fast-growing species could potentially grow equally well on soil where other species grew, as its growth strategy would promote fitness. Conifers fall at the other end of the spectrum. They put more energy into belowground biomass growth as this is the most efficient way for them to obtain nutrients (Li et al., 2021). They obtain most of their nutrients from the soil.

The importance of plant-soil feedback (PSF) relative to growth strategy in determining plant biomass is not fully understood. PSF is a mechanism where plants influence the composition and abundance of soil biota, as well as soil nutrients and other abiotic soil properties. This in turn can affect growth of other individuals of the same species, (Spitzer et al., 2021; Gundale & Kardol, 2021; Bever et al., 2012). Positive feedback occurs when a plant grows better in its own soil (referred to as conspecific soil) compared to a foreign soil (referred to as heterospecific soil), and negative feedback occurs when a plant grows worse in its own soil compared to a foreign soil (Bennett & Klironomos, 2018). Negative feedback is most commonly observed in experimental settings (Cortois et al., 2016; Kulmatiski et al., 2008; Bukowski et al., 2018). The strength of a PSF explains how much of an effect a plant species' own soil had on plant biomass. For example, larger negative feedback means that a plant species grows worse on its own soil relative to heterospecific soil compared to how it grew on its own soil relative to another heterospecific soil. PSF can be abiotic (e.g., through effects on the availability of soil nutrients and secondary chemicals present in the soil) (Bennett & Klironomos, 2018). Biotic PSF can occur from influencing the abundance of natural enemies and mutualists. Mutualists generally affect PSF positively for ectomycorrhizal (EcM) fungal species and can improve the negative PSF created from limitations in soil nutrients. Arbuscular mycorrhizal (AM) fungi generally produce negative PSF, however the dominant type in boreal forests is EcM (Revillini et al., 2016). Soil nutrient depletion causes negative PSF because it limits plant growth, but slow-growing boreal tree species can induce positive PSF by generating low-quality litter which does not add enough nutrients back into the soil for faster growing species with higher nutrient requirements (Bennett & Klironomos, 2018). To see the effects of biotic and abiotic properties on PSF, studies have been conducted where soil is sterilized (removing all microbes) and live inocula are added back into the soil (Kardol et al., 2006, Gundale et al., 2019). These studies also use live soils. This is done to determine the relative importance of biotic and abiotic soil properties for determining biomass. One approach to PSF experiments is to run a glasshouse experiment where the soil biotic community is experimentally manipulated. With this study design, live soil is collected from the study site(s) and used as an inoculum treatment for sterilized soil. This is done to control the biotic community in the soil independent of the abiotic properties in the soil. (Gundale et al., 2019). These studies use a two-experiment approach where the first experiment assesses seedling growth on live (not sterilized) soils from boreal forest sites, and the second experiment assesses seedling growth on boreal forest soils which have been sterilized and inoculated with soil from the boreal forest sites. The inoculation combinations are done where each sterilized soil is inoculated with each inoculum. Therefore, experiments which include both soil treatments allow for disentangling biotic and abiotic effects on PSF (Gundale et al., 2019).

Plant economic strategies could also determine how much biomass is invested in various tissues for resource acquisition (Baxendale et al., 2014). Generally, plant species range in a spectrum of plant economic strategies from resource-acquisitive to resource-conservative. Resource-acquisitive plants are those that are effective at obtaining resources, while resource-conservative species are slow-growing and have slow rates of tissue turnover (Gorné et al., 2022, Gundale & Kardol, 2021). Resource-acquisitive species often have high rates of photosynthesis, high concentrations of leaf and root nutrients, and high specific leaf area and specific root length (Lin et al., 2019; Wright et al., 2004; Freschet et al., 2010). Meanwhile, resource-conservative species often have a high C/N ratio, high concentrations of lignin, and high dry matter (Lin et al., 2019; Wright et al., 2004; Freschet et al., 2010). The plant economic spectrum is important for understanding PSF because it can influence the direction and strength of PSF (Gundale & Kardol, 2021). The review by Gundale & Kardol highlighted that resource-acquisitive species usually experience more negative PSF than resource-conservative species (Gundale & Kardol, 2021).

Here, we used a sterilization-inoculation experiment to determine biotic and abiotic PSF of four tree species (i.e., silver birch (*Betula pendula*), Norway spruce

(*Picea abies*), Scots pine (*Pinus sylvestris*), and Lodgepole pine (*Pinus contorta*)) with different plant economic and growth strategies. This was done in a two-stage experiment that included live and sterilized-inoculated soil. We did this to disentangle the roles of plant traits, biotic, and abiotic soil properties on PSF.

1.1 Hypotheses

1. In the live experiment, *B. pendula* seedlings will have the largest biomass and *P. abies* seedlings will have the lowest, because *B. pendula* has a 'fast' growth strategy relative to *P. abies*.
2. In the live experiment, each species will exhibit negative feedback (i.e., increased growth on heterospecific soil relative to conspecific soil), with these negative feedbacks being most severe for birch, and least severe for spruce. This is because negative PSFs are more common than positive PSFs, especially in fast-growing species (Cortois et al., 2016; Gundale & Kardol, 2021), and *B. pendula* is likely to have stronger negative PSF because it is a resource-acquisitive species that are generally less dependent on mycorrhizae for nutrient uptake (Jonczek et al., 2020).
3. In the sterilization-inoculation experiment, we expected the same patterns to emerge as in experiment 1, but with inoculum as the driver of PSF direction rather than sterilized soil origin. Inoculum is expected to affect PSF direction as strength of antagonistic microbes could result in negative feedback and mycorrhizal fungi could result in positive feedback (Bennett & Klironomos, 2019).

2. Materials and Methods

2.1 Site description and soil collection

Soil for each species was collected from Garpenberg in central Sweden and Svartberget in northern Sweden, in August 2022. The sites were established in 1992 and consist of replicated monocultures of different tree species. Soil in each plot (50 × 50 m) is therefore considered to be primarily "trained" by the planted tree species. This ensures that the soil biotic and abiotic properties are those found in connection with that tree species and should help determine the role of these properties in PSF of boreal tree species. Conspecific soil was collected from three replicate plots of *B. pendula*, *P. contorta*, *P. abie*s and *P. contorta* in Svartberget and three replicate plots for all species except *B. pendula* in Garpenberg. This is because only two replicates of *B. pendula* were established at that site. The organic soil layer and 2 cm of the surface mineral soil and was dug using a spade, sieved immediately (ø 10 mm) to remove rocks and large roots. The soil was then bagged and labelled and stored at 4°C until it could be used for the experiment. Soils from each replicate plot and species were kept separate and were used to form replicate blocks in the experiment.

2.2 Experimental Set-up

Two separate experiments were conducted, one with live soil (i.e., unsterilized) and one with sterile soil and an inoculum. Live soils are those which maintain all their biotic and abiotic properties as they have not undergone any type of sterilization. Sterile soils are those which were sterilized using gamma-irradiation (35 kGy) to remove all biotic properties in the soil. In the live soil experiment, there were four tree species, four species-specific live soil sources, and six replicates (five for *B. pendula*) for a total of 92 experimental units. Seedlings were planted in one-liter pots with a soil mixture of 50% oven-sterilized sand (120°C for 48 hours) and 50% live soil. Seedlings from each of the four tree species were planted in each of the four species-specific live soils so that each tree species was growing in each soil type (Figure 1). This resulted in 16 experimental units per replicate. They were then placed in a greenhouse for 5 months with six replicate blocks. The greenhouse conditions (pot) were kept consistent throughout the experiment and the plants were watered twice a week with each plant receiving the same amount of water (i.e., 50 ml for the first month to allow for seedling establishment, followed by 30 ml at each watering event).

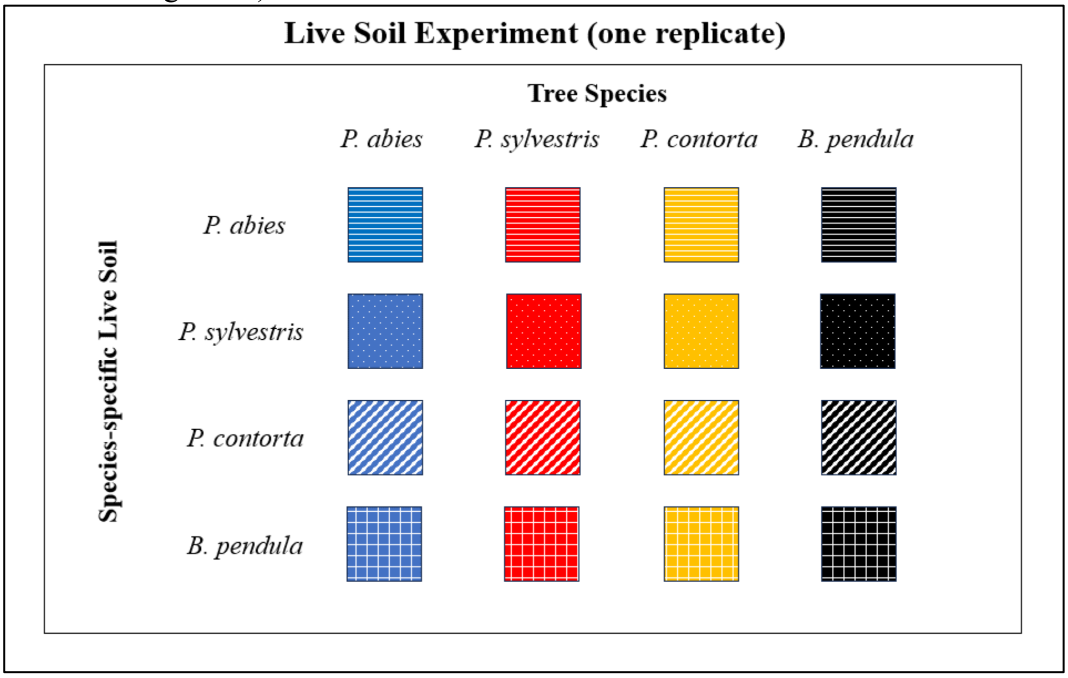

Figure 1. One replicate of the live soil experiment showing each combination of tree species planted and species-specific live soil. The colors correspond to the tree species planted and the patterns correspond to the species-specific live soil the seedling was planted in (n=6, except for n=5 for Betula pendula).

In the sterile soil experiment, there were four tree species, four sterilized soil sources, five soil inocula, and six replicates for a total of 448 experimental units. Seedlings were planted in one-liter pots with a soil mixture of 50% sand, 45% sterilized soil, and 5% soil inoculum. Each species was grown on sterilized soil, as well as sterilized soil with soil inoculum. Altogether, this resulted in 20 soil combinations for each tree species (Figure 2). Each tree species was grown on the 20 combinations of sterilized soil and/or soil inocula for comparison. As in the live experiment, pots were then placed in six replicate blocks and the experiment was conducted simultaneously in the same greenhouse as the live experiment. Plants from the live and sterile experiments were kept in the same greenhouse so that environmental conditions would be the same for each to allow for comparison between the two experiments. Further, one replicate from each experiment was placed so that the live and sterile experiments were right next to each other in the greenhouse in each block.

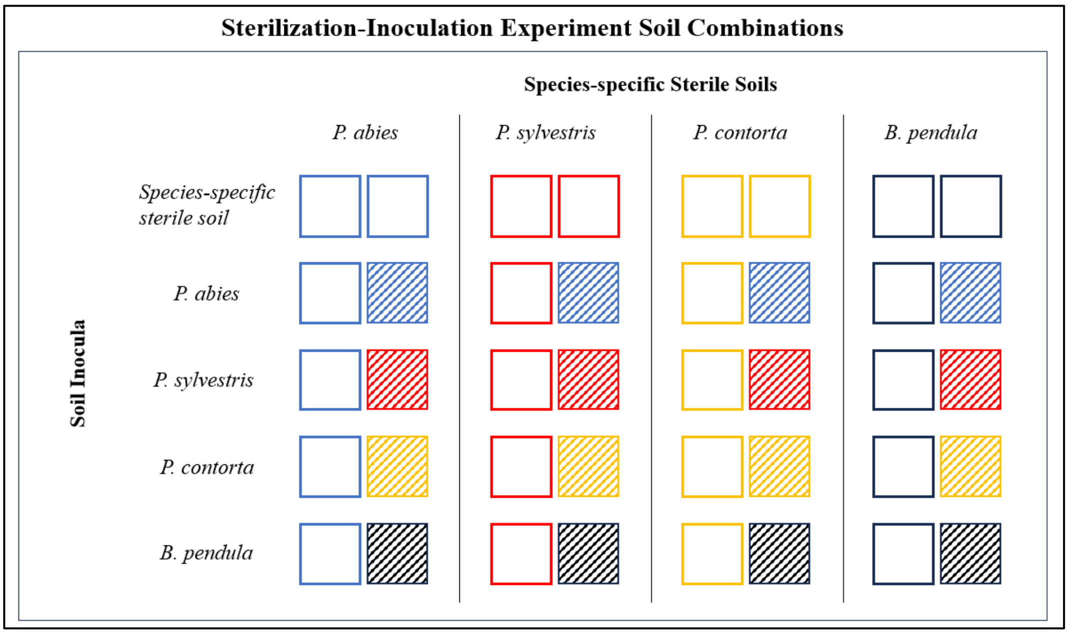

Figure 2. All soil combinations in the sterilization-inoculation experiment for one planted tree species in one replicate. Each pair of boxes represents one soil combination with the first box being the species of sterilized soil and the second box being the inocula. The boxes without a pattern represent the sterile soil and the boxes with a pattern represent the live inocula. Each species has been assigned a color for differentiation (n=6, except for n=5 for Betula pendula).

2.3 Plant Harvest and Data Collection

Seedlings were harvested from the greenhouse from February 27, 2023, to March 10, 2023 (five months after the experiment started). They were harvested beginning with the live experiment seedlings then the sterilized experiment seedlings and in order of planting at the beginning of the experiment. This ensured that data would stay consistent between the two parts of the experiment as all the live experiment seedlings were harvested around the same time and all the sterilized experiment seedlings were harvested around the same time. This was to reduce the chances that extra time in the greenhouse could affect seedling growth. The roots of each seedling were thoroughly washed when harvesting to remove all soil. This was done with an initial rinse under a tap with a spray nozzle to wash as much of the soil off as possible with a sieve underneath to catch any roots that detached. The seedling was then transferred to a pan with water in it to wash any remaining soil from the roots and pick out any dead root or soil fragments with tweezers. Once the roots were visibly clean the plant was cut to separate the above- and below-ground sections of the plant. These portions were placed in separate paper bags each labelled with the plant's identification code. At the end of each day, all harvested seedlings were placed in an oven at 60°C for 48 hours to fully dry. They were then stored at room temperature and weighed. Before being weighed, the samples were once again placed in the oven at 60°C overnight to evaporate any moisture that may have accumulated since being taken out of the oven after the initial drying. The above- and below-ground biomass was weighed separately, and these were added together to get the total biomass for each seedling. Weight was recorded in grams and put into an Excel spreadsheet.

2.4 Data Preparation and PSF Calculations

The total biomass for each seedling was calculated by adding the above- and below-ground biomass. The total biomass for each seedling was then log transformed to normalize the data to meet the assumptions for data analysis. In the live experiment, PSF was calculated by taking the log of the biomass in a species' own soil and subtracting the log of the biomass in a foreign soil (Cortois et al., 2016; Spitzer et al., 2022; Brinkman et al., 2010).

PSF = log (biomass in own soil) – log (biomass in foreign soil)

Positive PSF indicates that a species grows better on conspecific soils and negative feedback indicates that a species grows better on heterospecific soils. In the sterile experiment, PSF was calculated to compare the growth of plants in inoculum relative to the sterile soil origin. This was done by taking the log of the biomass of a fully sterile soil and subtracting the log of the biomass in the same sterile soil with a live inoculum.

PSF = log (biomass in sterile soil) – log (biomass in sterile soil with live inoculum)

Positive feedback indicates that a species grows better on the fully sterile soil and negative feedback indicates that a species grows better on the sterile soil with an added live inoculum.

2.5 Data Analysis

Data was analyzed in Excel and R by conducting ANOVA type III tests of variance with blocking effects, post hoc tests, and pairwise comparisons. Type III ANOVA was selected to account for the unbalanced experimental design.

2.5.1 Live Experiment

For the live experiment, data was analyzed in R (4.2.3) and Excel with an explanatory variable of soil origin and response variables of biomass and PSF. To evaluate the first hypothesis stating that *B. pendula* will have the largest biomass and *P. abies* will have the lowest, a boxplot was created in R to assess the mean biomass of each species. A bar plot of PSF was created in Excel to visualize results of the second hypothesis which states that each species will exhibit negative PSF. This figure shows whether a species had positive or negative feedback. A one-way ANOVA type III was used to determine whether the means of each species feedback are significantly different from one another. In this case, the one-way ANOVA was followed up by a Tukey post-hoc test to perform pairwise comparisons between species. The output shows us which species are significantly different from one another.

2.5.2 Sterilization-Inoculation Experiment

A three-way ANOVA type III was used initially to analyze the data from the sterilization-inoculation experiment using inoculum origin, sterile soil origin, and seedling species as fixed factors and block as a random factor. A three-way ANOVA is used to assess whether three different variables have an interaction effect, in this case tree species, soil origin, and soil inoculum. The ANOVA table shows each combination of the three variables and whether the interaction was statistically significant. From here, post hoc tests were conducted to further understand which interactions were significant.

A one-way ANOVA type III was used to further explore the relationship between feedback and soil origin for each tree species as this was the only significant result from the three-way ANOVA. Data was grouped by species and the effects of soil origin on feedback was analyzed as this was the only significant result. Though this hypothesis set out to determine the role the soil inocula played in PSF, the findings suggest that soil origin is significant, so that was explored.

3. Results

3.1 Live Experiment

3.1.1 Hypothesis 1

B. pendula exhibited a significantly higher mean biomass than the other three species (Figure 3.). Additionally, *P. abies* had a lower biomass than *P. sylvestris* and *P. contorta,* but it was not significantly lower. There were no observed significant differences in biomass among the other tree species.

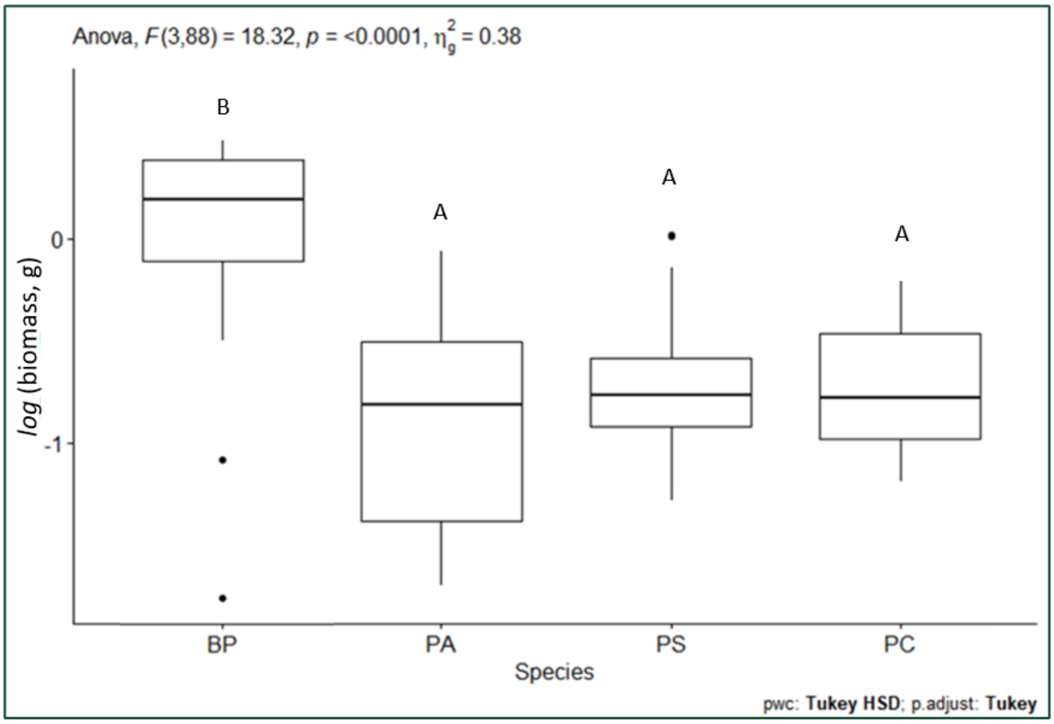

Figure 3. Boxplot showing the results of an ANOVA type III test. BP, B. pendula; PA, P. abies; PC, P. contorta; PS, P. sylvestris. Dots indicate biomass values significantly different from zero at α=0.05. The horizontal bars show the median and the vertical lines show the 95% confidence interval.

3.1.2 Hypothesis 2

In the live soil experiment, *P. contorta* had positive feedback of 0.16±0.09 ($p<0.05$), *B. pendula* had neutral feedback, and *P. abies* and *P. sylvestris* had negative feedback of -0.26±0.11 ($p<0.05$) and -0.26±0.09 ($p<0.05$) respectively. However, only *Pinus sylvestris* and *Picea abies* had significant PSFs.

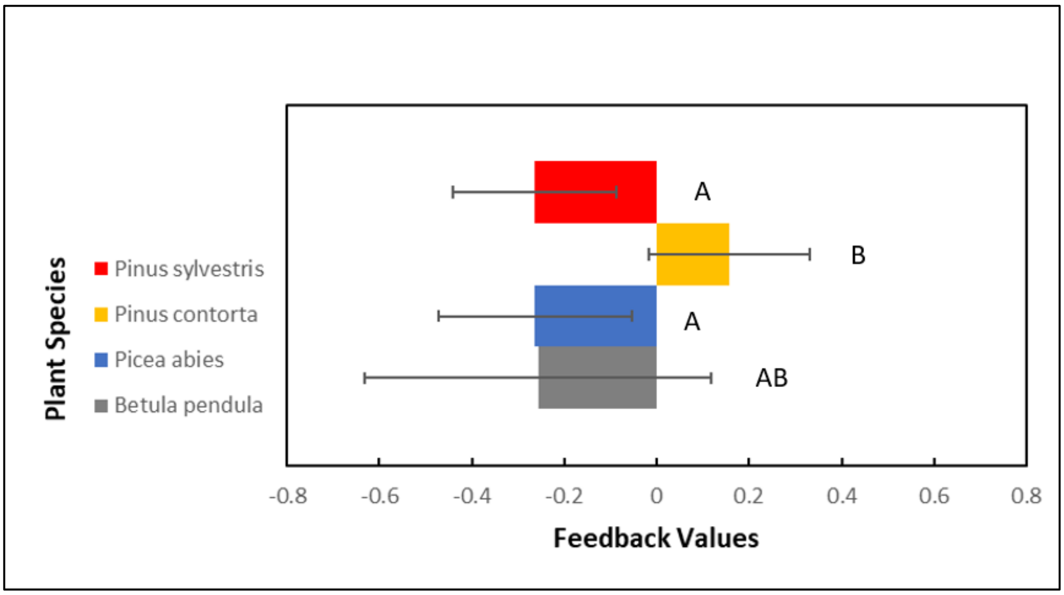

Figure 4. Bar plot showing plant-soil feedbacks in four boreal tree species. Bars are mean values with 95% confidence intervals. In post-hoc tests the relationship between feedback values was statistically significant ($F=3.23$; $p=0.028$; $\eta_g^2=0.13$) and the letters at each bar show pairwise comparisons.

3.2 Sterilization-Inoculation Experiment

3.2.1 Hypothesis 3

Soil inocula did not have a significant effect on PSF for any of the tree species. However, there was a significant species-soil origin interactive effect (Table 1).

Table 1. ANOVA table for PSF with block as a random effect. Soil origin refers to sterilized soil origin and inoculum is 5% live soil from the various species.

Effect	DFd	F	p	P<0.05
Species	292	2.284	7.90e-02	
Soil Origin	292	0.811	4.89e-01	
Inoculum	292	0.647	5.85e-01	
Species: Soil Origin	292	7.363	1.11e-09	*
Species: Inoculum	292	0.237	9.89e-01	
Soil Origin: Inoculum	292	0.553	8.35e-01	
Species: Soil Origin: Inoculum	292	0.834	7.06e-01	

Because of the significant result of species and soil origin on PSF in the 3-way ANOVA, we ran individual 1-way ANOVAs of feedback ~ soil origin for each tree species (Figure 5.). There was a significant relationship between species and sterilized soil origin for all tree species except for *B. pendula* (Table 2; Fig. 5). For the remaining species, there were both positive and negative PSF values for each sterilized soil origin. *P. abies* had a significant relationship between species and sterilized soil origin, but post hoc tests did not identify any significant differences between each sterilized soil origin. The feedback was more positive when grown with sterilized soil from *P. contorta* than when grown on sterilized *P. sylvestris* soil, but it was not significant. *P. contorta* had a significant difference in PSF between sterile soils from *P. abies* and *P. sylvestris* and from *P. abies* and *B. pendula*. The most positive PSF was found for *P. contorta* on sterilized *P. abies* soil, whereas individuals had more negative PSF when grown with sterilized soil from *P. sylvestris* and *B. pendula*. *P. sylvestris* had a significant difference in PSF between sterile soils from *B. pendula* and *P. abies* and from *B. pendula* and *P. contorta.* There was no difference in PSF for *B. pendula* soil for the various soil origins.

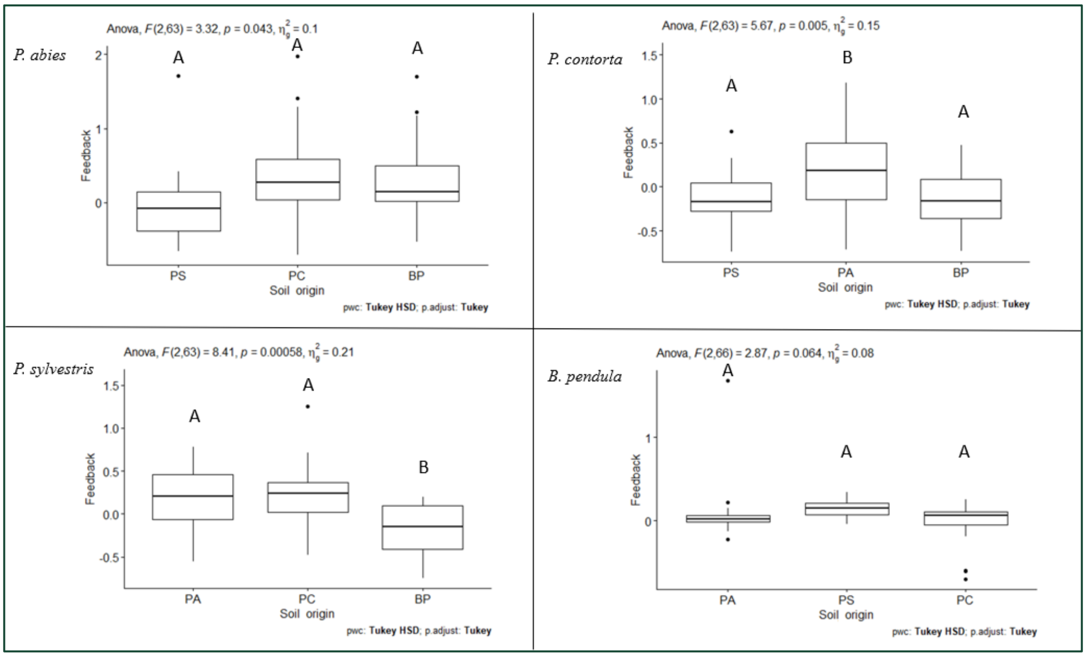

Figure 5. Figures showing the results of one-way ANOVAs of species ~ soil origin (P. abies (PA); P. contorta (PC); P. sylvestris (PS); B. pendula (BP)) for each tree species in the sterilization-inoculation experiment. Post-hoc tests are included for each as letters above the bars.

Table 2. ANOVA table for the 1-way ANOVA of feedback ~ soil origin in the sterilization-inoculation experiment. Soil origin refers to sterilized soil origin. BP, B. pendula; PA, P. abies; PC, P. contorta; PS, P. sylvestris.

Species	Effect	DFd	F	p	P<0.05
PA	Soil Origin	63	3.316	0.043	*
PC	Soil Origin	63	5.673	0.005	*
PS	Soil Origin	63	8.412	0.000578	*
BP	Soil Origin	66	2.868	0.064	

4. Discussion and Conclusions

This research was done in the context of boreal tree species used in forestry operations in northern Sweden. PSF research is important in this field because it can inform management decisions and best practices for planting after harvest. Knowing the way a species grows on soil conditioned by heterospecifics and conspecifics can help determine what is best to plant on a harvested plot or an area that is being reforested. PSFs are complex with many different factors that could affect tree growth. This is seen in the range of results shown in this study with some trees exhibiting positive PSFs and others negative PSF. None of the hypotheses were completely supported. The first two were partially supported, and the third was rejected. These differences from what was expected demonstrate how it is not easy to predict PSF based on one factor and how many different factors need to be considered to determine how a species will grow in a soil and what is best to plant in an area.

The first hypothesis predicted that *B. pendula* would have the largest biomass growth and *P. abies* would have the smallest biomass mass growth due to their growth strategies. We also expected the two *Pinus* species to fall in the middle. This hypothesis was partially supported because *B. pendula* had significantly higher biomass growth than the other species, but *P. abies* did not have significantly lower biomass. However, *P. abies* did have the lowest average biomass. This falls in line with the growth rates of these species as it is known that *B. pendula* is a fast-growing species and *P. abies* is a slow-growing species (Li et al., 2021). This result also follows the plant economic spectrum as the species that allocated more to above-ground biomass had the highest total biomass (Li et al., 2021; Baxendale et al., 2014). This allows *B. pendula* to be faster growing, and in turn have greater overall biomass. These results therefore point to the importance of plant growth strategy in ecosystem productivity. Specifically, *B. pendula* might be a useful species for biomass accumulation after clear cuts or for restoration in boreal forests.

The second hypothesis states that each species will exhibit negative PSF and that they will be most severe for *B. pendula* and least severe for *P. abies.* This is due to its resource-acquisitive strategy. Gundale & Kardol (2021) suggested that resource-acquisitive species usually experience more negative PSF than resource-conservative species. However, this was not supported for this hypothesis in this experiment (Gundale & Kardol, 2021). All species experienced negative PSF except for *P. contorta,* but the only significantly negative PSF was seen in *P. abies* and *P. sylvestris*. *P. abies* is a resource-conservative species, but *P. sylvestris* is relatively more acquisitive. *B. pendula,* the resource-acquisitive species, did not have a significant negative PSF. There were also no significant differences in PSF direction between *B. pendula* and the other species, further not supporting the hypothesis. *P. contorta* did follow this pattern as it is in the middle of the acquisitive-conservative spectrum and experienced positive PSF. However, the differences seen in PSF of *P. contorta* may be due to other factors such as *P. contorta* being an exotic species (Gundale et al., 2014). It establishes easily in new areas and seems to grow better in its own soil. This may be due to a difference in the microbial community and mutualists of the exotic species compared to the native species (Gundale et al., 2014). For example, according to the enemy release hypothesis the antagonistic microbes that would result in negative feedback would not be present in the new range (Gundale & Kardol, 2021). In addition, the positive PSF may also be driven by abiotic factors in the soil such as its ability to associate with nitrogen fixers, its ability to obtain phosphorus, or its ability to otherwise engineer the soil in a way that leads to positive PSF through depletion of other nutrients (Beals et al., 2020).

The third hypothesis focused on the sterilization-inoculation experiment and whether feedback is driven by biotic or abiotic factors. It was predicted that the species would follow the same trend as the second hypothesis with soil inoculum as the driver rather than soil origin. This was not supported as soil inoculum had no effect on PSF, but soil origin did. For *B. pendula* there was no difference in PSF related to the various inoculation treatments which may be due to its greater ability to "do it itself" and its greater plasticity since it is fast-growing (Jonczak et al., 2020; Ibáñez et al., 2022). It is also a pioneer species, so it has evolved to grow well in a wide range of soil conditions. The significant effect of sterilized soil origin on PSFs indicates that abiotic factors are more at play as there is no biotic community in the sterilized soil. Plants deplete nutrients from the soil, but they may not be the same nutrients in the same amounts for each tree species. This may explain the trend seen in this experiment where each tree species had better growth in away soils. Growth in another species' soil may allow trees to tap into a different pool of nutrients like nitrogen and phosphorus, which enhance their growth. Each species may have a nutrient niche which can cause certain nutrients to pool if they are not being used by that species, thus making those nutrients available to another species planted in that soil (Nitschke et al., 2016). These nutrient pools could be due to rooting depth or trees selectively using different forms of nitrogen and phosphorus (Nitschke et al., 2016). The significant effects seen between different soil origins for *P. sylvestris* and *P. contorta* could be caused by differences in the nutrient pools for those sterilized soil origins. For instance, the significant relationship between *P. abies* planted in sterile soils from *P. sylvestris* and *P. contorta* may be due to differences in the availability of certain nutrients caused by one being a native species and one being an exotic species. This pattern was also seen in *P. contorta* with significant relationships between the different sterile soils. In the end, the abiotic factors at play in the soil are most responsible for the PSF observed in this experiment.

The first two hypotheses were partially supported, and the third hypothesis was rejected. It can be concluded that plants that are fast-growing and focus on above-ground biomass will have greater biomass than species that are slow-growing and focus on below-ground biomass. Growth rate and plant economics spectra might be the main drivers of this. This was shown with *B. pendula* having significantly higher growth than the other three species. Additionally, in the live experiment we found that *P. contorta* grows better on conspecific soils while the other three species grow better on heterospecific soils. This partially proves the second hypothesis as three of the four tree species exhibited negative PSF. This is likely due to *P. contorta* being an exotic species and establishing easily in this region. Lastly, it can be concluded that the soil inocula had no significant effect on tree growth thus rejecting the third hypothesis. The best indicator of PSF was sterile soil origin. The results from these experiments show that both the biotic and abiotic communities can affect PSF and that a combination of soil nutrients and plant growth strategy is responsible for PSF.

This work has many implications for the forest industry and future research. The findings can be valuable to the forest industry by informing more sustainable timber harvesting, supporting the use of crop rotations, and informing reforestation or afforestation practices. Additionally, this research shows the importance of maintaining soil health and protecting soil quality in forestry practices as soil nutrients play a big role in PSF. Lastly, it shows the importance of proper species selection for forest plantings. It can be a good idea to plant a different species from the one harvested or to introduce *P. contorta* as it does well as a pioneer species. Crop rotation would likely increase growth of *P. abies* most as it exhibited negative PSF and is resource-conservative and slow-growing. Giving it access to a new pool of nutrients can be beneficial compared to *B. pendula* which grows well on any soil. Managers can use a combination of growth strategy, soil nutrients, and plant-soil feedback to inform species selection in forest planting to attain the best yield. More research is needed in the field of PSF so that managers can continue to make the best-informed decisions about adaptive management strategies and the long-term sustainability of the forest industry.

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Popular science summary

Boreal trees have different growth strategies that range from slow growing to fast-growing. This is important because it tells us how fast plants are able to gain biomass under similar conditions. This study used four boreal tree species that ranged from slow-growing Norway Spruce (*P. abies*) to fast-growing Silver Birch (*B. pendula*). This allowed us to see how trees with different growth strategies and soil communities grew on each soil. The main focus of this study was on plant-soil feedback (PSF). This is a mechanism where plants influence the make-up and abundance of soil biota and soil nutrients and other abiotic properties. This can then affect the growth of other trees on that soil. There can be positive or negative feedback. Positive feedback means that a plant grew better on its own soil and negative feedback means that a plant grew better on soil conditioned by another species. Negative feedback tends to occur more often than positive feedback.

This study used four boreal tree species which were silver birch (*Betula pendula*), Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), and lodgepole pine (*Pinus contorta*). These were used because they have different growth strategies and plant economic strategies. Soil was collected from two different sites in Sweden called Garpenberg and Svartberget. Two separate experiments were set up to test how different factors in the soil affect plant growth. The first experiment used live soil which keeps its biotic and abiotic properties. This experiment involved growing each of the four tree species on soil from each of the four species. This gave us 16 combinations of tree and soil. In the sterilization-inoculation experiment, each soil was sterilized using gamma-irradiation. Then, different live soils were added back in as inoculum. The sterilization removed all of the living things from the soil and left the abiotic properties. This allows us to see how the abiotic properties affect tree growth compared to the biotic properties. There were four tree species, four sterilized soils, and five inocula. The inocula are live soil from each of the four tree species and then sterilized soil from whichever sterilized soil is being used. This allowed us to compare the effects of the inocula to a control. After five months growing on the various soil combinations, the plants were harvested, dried, and weighed. Feedback was then calculated by subtracting the average biomass of a species in foreign soil from the average biomass of that species in its own soil. The same goes for the sterilization-inoculation experiment except the average biomass with live inoculum was subtracted from the biomass in just sterile soil. Data was then analyzed using a computer program called R.

Hypothesis 1 and 2 covered the live experiment and hypothesis 3 covered the sterilization-inoculation experiment. Hypothesis 1 said that birch will have the highest biomass and spruce will have the lowest. Birch had significantly higher biomass than the other species, but spruce did not have significantly lower biomass. Hypothesis 2 said that each species in the live experiment will have negative feedback because they are more common than positive feedback. All species had negative feedback except lodgepole pine. This may be because it is not native to Sweden and is a pioneer species. Hypothesis 3 said that the sterilization-inoculation experiment shows the same pattern as hypothesis 2, but the soil inocula will be the reason for the pattern. The soil inocula ended up having no effect on feedback for each species, but sterile soil origin did. There was a significant relationship between species and sterile soil origin for spruce and both pine species. Lodgepole pine had significantly better growth on spruce soil and Scots pine had significantly worse growth on birch soil.

Overall, the first two hypotheses were partially supported, and the third hypothesis was not supported. The results of the first hypothesis fall in line with the growth rates of those species. Birch has the fastest growth rate and the highest biomass. This points to birch being a useful species for accumulating biomass after a clear cut or for restoration in boreal forests. The results of the second hypothesis showed that the non-native species, lodgepole pine, had positive feedback and the rest had negative feedback. Scots pine and spruce had significantly negative feedback. The results of the lodgepole pine may be because it's an exotic species. It can establish and grow better in its own soil likely due to a difference in the microbial community of this species. The third hypothesis was rejected because inoculum did not affect growth. Birch also saw no difference for each sterile soil origin. This may be because it is a pioneer species which allows it to easily establish anywhere. Plants deplete nutrients from the soil, but they may not be the same nutrients for every species. This is why some species grow better on the soil of other species. Abiotic factors are most responsible for observed feedback in this experiment.

Overall, the results show that both biotic and abiotic communities in the soil can affect feedback. A combination of soil nutrients and microbes and plant growth strategy is most responsible for PSF. This work has implications in the forestry industry by informing more sustainable timber harvesting, supporting the use of crop rotations, maintaining soil health, protecting soil quality, and showing the importance of proper species selection for the soil community present. Managers can use a combination of growth strategy, soil nutrients, plant-soil feedback, and past growth history to make informed decisions about management strategies and long-term sustainability.

Acknowledgements

I would like to thank my thesis supervisors Clydecia Spitzer and Michael Gundale for their guidance and assistance with this master thesis project. I would also like to thank Ilse van Duuren for her assistance with harvesting plants from the greenhouse and watering plants while they grew in the greenhouse. I would also like to thank my family and friends for their support, I truly would not have been able to do it without them.

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