To grow, or not to grow: Mode of action of plant growth promotion by the fungus *Clonostachys rosea*

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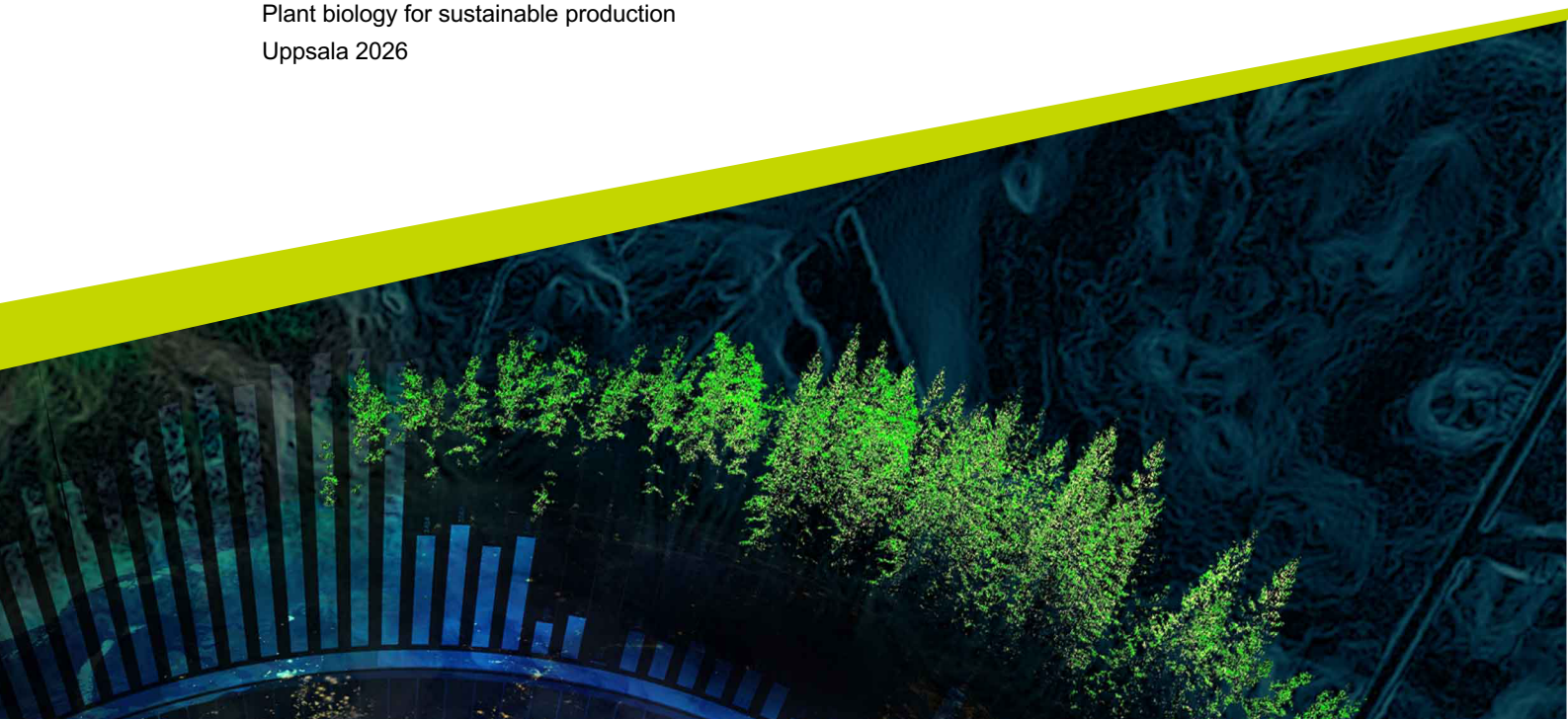
Degree project/Independent project • 30 credits
Swedish University of Agricultural Sciences, SLU
Forest Mycology and Plant Pathology
Plant biology for sustainable production
Uppsala 2026



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Credits:	30 credits
Level:	A2E
Course title:	Independent project in Biology, A2E
Course code:	EX0856
Programme:	Plant biology for sustainable production
Course coordinating dept:	Forest Mycology and Plant Pathology, Agricultural Plant Pathology
Place of publication:	Uppsala
Year of publication:	2026

Keywords:	Clonostachys rosea, Intraspecific variation, Plant-beneficial fungi, Plant growth promotion, Wheat

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Abstract

The use of plant-health-promoting microorganisms in agriculture is a sustainable way to achieve higher yields. *Clonostachys rosea* is a fungal biocontrol agent that can promote plant growth, but the nature of the interaction is unknown. This project investigated if this plant-fungal interaction is direct or indirect by inoculating wheat and *Arabidopsis thaliana* with six *C. rosea* strains – three with promoting effects and three with no effects – and observing plant growth parameters and root architecture. For wheat, inoculation with plant health promoting strains resulted in increased shoot and seedling fresh weight ($p<0.05$), however no differences in root length or lateral root number were recorded. In *A. thaliana* inoculation with a growth-promoting strain led to significantly shorter and less branched roots ($p<0.05$) Interestingly, inoculation with a non-promoting strain resulted in plants with roots significantly longer than promoting strains ($p<0.01$). In contrast to growth promotion, fluorescence microscopy using a YFP auxin reporter *A. thaliana* lines revealed that non-growth promoting strains had auxin fluorescence comparable to control while promoting strains had visibly higher fluorescence. To investigate indirect effects bioassays using metabolite fractions of three *C. rosea* strains were conducted. They revealed that the strains contain different antimicrobial compounds against *Pseudomonas syringae, Escherichia coli, Botrytis cinerea* and *Saccharomyces cerevisiae.* Our findings point to a species and strain specificity of plant growth promoting effects by *C. rosea*. In wheat the results indicate an indirect interaction, contrary to *A. thaliana* where a direct interaction is more likely.

Keywords: Clonostachys rosea, Intraspecific variation, Plant-beneficial fungi, Plant growth promotion, Wheat

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Abbreviations

PHP	Plant health promoting
VOCs	Volatile organic compounds
dpi	Days post inoculation

1. Introduction

The use of plant-health-promoting microorganisms in agriculture is an attractive way to achieve higher yields while keeping sustainability in mind, enabling us to avoid the increased disease pressure, pesticide resistance and negative health effects that traditional pesticide use is characterised by. Two fungal genera of interest are *Trichoderma* and *Clonostachys*, both harbouring species that are used as biological control agents; living agents that protect crops from pests or pathogens. Species from these genera have shown the ability to promote plant growth, meaning that they can provide dual benefits for the agriculture industry. These microorganisms are commonly referred to as plant-growth-promoting but in this project, they will be referred to as plant-health promoting (PHP). This term includes not only direct growth promotion by the microorganism but also indirect interactions that benefit the overall health of the plant. Examples of direct interactions include secreting hormone-like compounds which alter plant gene expression and result in increased growth (Taheri et al. 2025). A direct interaction could also be a microorganism that primes the plant: inducing its defence responses and keeping the plant on high alert, resulting in quicker activation of defences against pathogens; increasing its chances of survival. An example of an indirect interaction could be a microorganism in the rhizosphere that outcompetes a pathogenic microorganism, thereby protecting the host plant. Extensive research on *Clonostachys* species has proved their many useful properties, but little is known about the underlying mechanisms, in particular the mechanisms of plant growth promotion. While not knowing if the interaction is direct or indirect does not change the result – a healthier and higher yielding plant – understanding the nature of the interaction makes us able to utilise these microbes as efficiently as possible.

1.1 Clonostachys rosea

Clonostachys rosea is an ascomycete that is primarily found in the soil. It is a mycoparasite that consumes other fungi for nutrients, providing a direct method of controlling plant pathogens. *C. rosea* has shown ability to control plant pathogenic fungi like *Botrytis cinerea*, *Fusarium graminearum* and plant parasitic nematodes like *Meloidogyne incognita* (Hasan et al. 2022; Khairullina et al. 2023; Stucky et al. 2024). Part of its success as a biological control agent is due to its generalist lifestyle. *C. rosea* can colonise all parts of the plant and live endophytically without causing harm to the host plant (Chatterton et al. 2008; Chatterton & Punja 2012). When *C. rosea* colonises wounds in plant tissues it will not spread to surrounding healthy tissues like a pathogenic fungus would. This effectively makes it a living barrier that protects the plant towards pathogens

(Chatterton & Punja 2012). It is also very competitive and able to colonize the rhizosphere quicker than other microorganisms. It is believed that this is due to its ability to compete with other microorganisms for essential nutrients and space (Nagaraj & Kolanthasamy 2025). Another component central to *C. rosea's* success is its large arsenal of secondary metabolites with antimicrobial properties, enabling it to conquer prey and competitors through antibiosis (Köhl & Ravensberg 2021). Compared to other fungal species with similar lifestyles *C. rosea* has a higher number of genes coding for polyketide synthases; genes important for pigment production and normal growth but also central to antagonism towards other fungi (Fatema et al. 2018). While *C. rosea* can directly parasitise nematode eggs, secreted metabolites also interfere with normal nematode development (Shravani et al. 2026). When exposed to *C. rosea* culture filtrates from strain PHP1701, egg development was delayed and motility of juvenile nematodes were reduced (Stucky et al. 2024). Culture filtrates from strain IK276 significantly increased nematode mortality (Iqbal et al. 2018).

This generalist lifestyle makes *C. rosea* an ideal candidate for an integrated pest management approach. It can adapt to different environments and hosts, it is effective against a large range of pathogens and pests, and it has multiple modes of action; making it harder to overcome. It also has the added benefit of being able to detoxify mycotoxins like deoxynivalenol and zearalenone, a very attractive trait for a biocontrol agent (Kosawang et al. 2014; Khairullina et al. 2023). Some strains of *C. rosea* have also been shown to have plant growth promoting effects, which would be yet another benefit to reap from utilising this fungus.

1.2 Plant health promotion

PHP-microorganisms can promote plant health in many ways. VOCs from plant pathogens have been shown to reduce plant growth (Chen et al. 2024), and compounds from *Clonostachys* and *Trichoderma* species have been shown to have PHP effects; affecting both growth and defence against pathogens without any physical contact between the fungi and plant. *C. rosea f. catenulata* VOCs have shown growth promoting effects on *Arabidopsis thaliana*, increasing root length, lateral root number and length, and above ground fresh weight (Wu et al. 2026). Exposure to *T. viride* VOCs resulted in taller *A. thaliana* plants with more lateral roots (Hung et al. 2013). *Trichoderma* volatiles show a dose dependent relationship in *A. thaliana*, where lower concentrations promote growth but higher concentrations inhibit it (Kottb et al. 2015). In *Trichoderma* species it has been observed that colonisation of the plant changes root architecture by making the roots longer (Contreras-Cornejo et al. 2024). This would facilitate water and nutrient uptake and could be an example of direct interaction with PHP-effects.

PHP microorganisms are also known to promote growth through changes in plant hormone levels. A well-known example is the enzyme ACC-deaminase, which cleaves ethylene precursors and prevents ethylene from being formed. Ethylene is a plant hormone involved in many central processes in the plant, one of them being stress regulation. When under stress, like drought or changes in salinity, the plants will produce ethylene that in turn inhibits plant growth. Inoculation of a plant with an ACC-deaminase producing microorganism could help overcome this growth inhibition. Certain *Trichoderma spp.* can produce ACC-deaminase. Inoculation with *T. asperellum* enhances wheat tolerance to stress caused by waterlogging and results in increased yields (Rauf et al. 2021). *C. rosea* can promote tomato growth by secreting auxin (Han et al. 2022) and *Trichoderma* promotes *A. thaliana* growth through auxin dependent mechanisms (Contreras-Cornejo et al. 2009). Transcriptomic analysis has revealed that *C. rosea* upregulates genes involved in auxin signalling in *A. thaliana* (Yu et al. 2025). Modulating plant architecture by affecting hormone levels is another example of a direct interaction

Another way that microorganisms can promote growth is through activation of plant defences. *C. rosea* has the ability to induce genes related to defence responses in tomato and wheat (Roberti et al. 2008; Kamou et al. 2020). This is thought to lead to activation of induced systemic resistance (ISR), a state of heightened alert that enables the plant to respond quickly to attack by pathogens or pests (Choudhary et al. 2007). However, how this activation of defence genes by *C. rosea* lead to triggering ISR is not yet understood (Nagaraj & Kolanthasamy 2025).

C. rosea shows strain-to-strain variation in growth promoting effects, highlighting the need to explore different combinations of strain and plant species to find an optimal combination (Sun et al. 2020). Evidence also points to a species-specificity of PHP-effects, meaning that two plant species that are both being promoted can have differing effects. An example of this is *C. rosea* promoting root length in rice but not in *A. thaliana.* The *A. thaliana* plants did however still exhibit other PHP-effects such as an increase in biomass and visibly more vigorous plants (Chen et al. 2024). These findings indicate that *C. rosea* interacts with plants in different ways depending on species and that growth promotion can look different in different plants.

The underlying cause of PHP by *C. rosea* in wheat is still being investigated. It is uncertain whether these effects are due to direct interaction between the plant and fungus, for example by changing gene expression to promote growth or by secreting hormone-like compounds that alter the plants growth. The effects could

on the other hand be due to indirect interaction, as these fungi are adept at outcompeting other microorganisms in the soil or rhizosphere and able to consume harmful fungi. A reduction of pests and pathogens could be responsible for an increase in growth due to the growth-defence trade-off. This trade-off its believe to be caused by the increased demand of resources the plant has to spend on defensive measures and the crosstalk of growth and defence signalling molecules inhibiting each other (He et al. 2022).

1.3 Aim of project

As PHP effects seem to vary depending on plant species, dose of compound and strain of fungi, finding suitable strain-species combinations is key to reap the benefits of *C. rosea's* plant growth promoting abilities. It is of interest to investigate the mechanism of promotion, to be able to harness these beneficial effects. *C. rosea* has been demonstrated to have PHP effects on wheat, but the nature of the interaction is not yet known. There are indications of strain-to-strain variation and genotype x genotype interactions between fungal strain and plant cultivar. This project investigated the strain-to-strain variation in plant growth promotion ability of six *C. rosea* strains, aiming to answer if plant growth promotion is due to direct interaction between the plant and the fungi. This was done *in vitro* using spring wheat cultivar 'Happy' and two ecotypes of *Arabidopsis thaliana*: wildtype col-0 and a col-0 mutant carrying the auxin reporter DR5-VENUS. The six *C. rosea* strains used for this project were categorised as PHP / non-PHP based on previous findings (Table 1). Strains vary in pigmentation, pigment colour and growth pattern (Figure 1). Metabolite extracts were used to compare the strains antimicrobial activity.

Research question:

- Is plant growth promotion by *Clonostachys rosea* due to direct interaction between the plant and the fungus?

Hypotheses:

- ❖ Growth promotion of wheat is due to direct interactions with the fungus
- ❖ *C. rosea* inoculation causes changes in wheat root architecture
- ❖ *C. rosea* can promote growth in *A. thaliana*
- ❖ *C. rosea* affects auxin expression in *A. thaliana*
- ❖ Both non-PHP and PHP strains will show antimicrobial activity
- ❖ Which fractions show antimicrobial activity will differ between Non-PHP and PHP strains

2. Materials and Methods

2.1 *C. rosea* strains

Six strains of *C. rosea* were used for inoculation (Fig 1). The strains were chosen based on previous soil experiments on wheat (unpublished) where they were classified as PHP/non-PHP. Three PHP strains and three non-PHP strains were selected (Table 1).

Table 1. The strains used in this project, categorized based on previous findings

Strain	Category
1885	PHP
1882	PHP
GR31	PHP
GR3	non-PHP
902.72E	non-PHP
2176	non-PHP

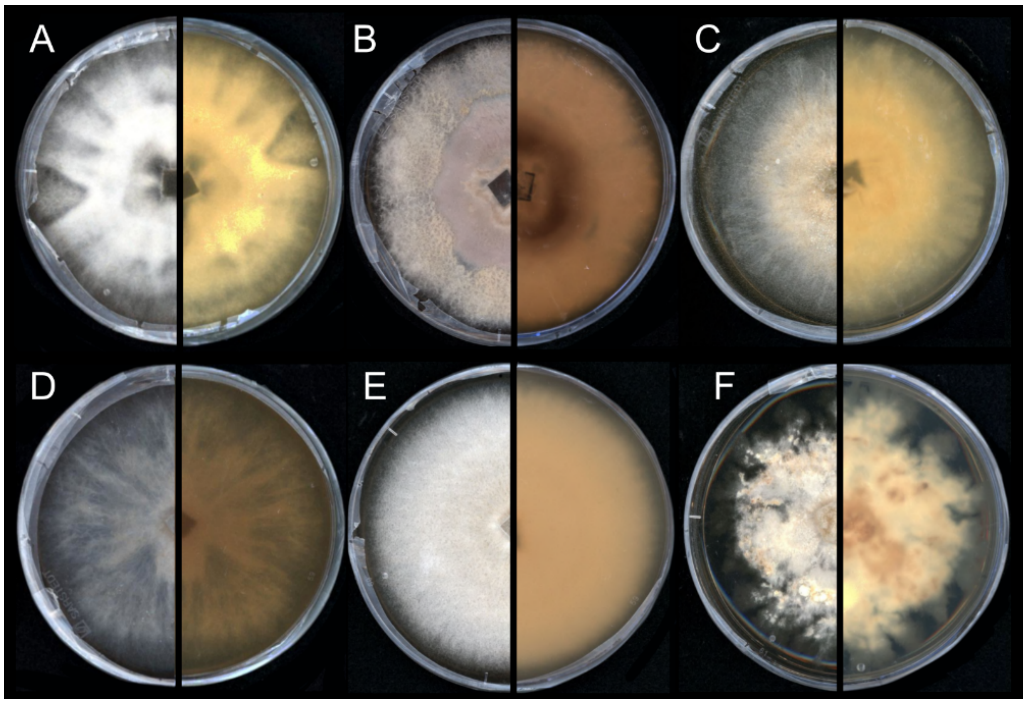

Figure 1: C. rosea strains used in the project. The left side shows the plate viewed from above, the right side shows plate viewed from below. ***A.*** *1882* ***B.*** *GR31* ***C.****1885* ***D.*** *GR3* ***E.*** *902.72E* **F.** *2176. The strains showed variation in growth patterns, pigment colour and pigment accumulation.*

2.2 Seed sterilization and cultivation.

2.2.1 Wheat cultivar 'Happy'

Spring wheat cultivar 'Happy' was chosen based on previous experiments with *C. rosea*. Seeds were washed using water and detergent at 170 rpm for 10 minutes, rinsed with sterile water, washed with 3% NaOCl at 170 rpm for 15 minutes and finally rinsed with sterile water thrice. After washing, the seeds were dried overnight in the dark at 20°C. Wheat seeds were always grown on 0,8% BactoAgar (Saveen Werner).

2.2.2 Arabidopsis thaliana

Seeds were submerged in 95% ethanol for 2 minutes, rinsed with sterile water, suspended in 80% ethanol for 10 minutes and washed thrice with sterile water. *A. thaliana* seeds were grown on ½ MS media, pH 5,8, containing 2,2 g/L Murashige-Skoog (Duchefa), 10 g/L sucrose (Duchefa) and 1% Plant Agar (Duchefa).

2.3 Microbe cultures

2.3.1 *Clonostachys rosea* and *Botrytis cinerea B.05.10*

C. rosea and *B. cinerea* were grown on Potato dextrose agar (VWR) in the dark at 25°C. Spores were harvested by pipetting 4 mL of ddH_2O onto the plate and carefully aspirating without disturbing the mycelia until the water turned turbid. Spore concentration was determined using a hemacytometer (Hausser-Scientific) and the following formula:

no. of spores in 5 squares/ 0.02 *1000 * dilution factor = spores/mL

2.3.2 Saccharomyces cerevisiae AH109

S. cerevisiae was grown on YPAD media, containing 10g/L yeast extract, 20g/L peptone, 10g/L glucose and 0,04g/L adenine sulfate. The plates were incubated in 30°C. Liquid cultures were made by adding 1 colony to 10 mL liquid YPAD media. Tubes were incubated in 30°C, shaking at 200 rpm. Concentrations were determined by measuring OD_{600}.

2.3.3 *Pseudomonas syringae DC3000* and *Escherichia coli* TOP10

P. syringae and *E. coli* strains were grown on LB media, pH 7.0, containing 10g/L Bactotryptone (BD), 5g/L granulated yeast extract (Millipore), 10g/L NaCl (Duchefa) and 15g/L agar BactoAgar (Saveen Werner). Liquid cultures were

made by adding 1 colony to 10 mL liquid LB media. Tubes were incubated in 37ºC shaking at 150 rpm Concentrations were determined by measuring OD_{600}.

2.4 Wheat root inoculation

Surface sterilized 'Happy' seeds were plated on 0.8% BactoAgar. Plates were sealed with parafilm and placed vertically in the dark at 20ºC for 3 days. Roots were inoculated with *C. rosea* via dipping for 10 seconds in spore solutions containing 10^7 spores/mL. Dipping in water was used as control treatment. 16 seedlings/strain were inoculated and grown in the dark at 20ºC. After 4 days of inoculation plates with inoculated seedlings were moved to climate chambers with short day conditions. Roots were imaged 4- and 6-days post inoculation using a Plustek OpticPro A320E scanner and digital measurements were taken using Fiji (https://imagej.net/software/fiji/). 6 days post inoculation the seedlings were harvested, root and shoot weight was measured and lateral root number was counted. The seedlings were dried at 50ºC overnight and stored at room temperature until dry weight was measured.
When repeating this experiment the procedure was modified by shortening the germination time to 2 days and after inoculation seedlings were immediately placed in the climate chambers. 30 seedlings/strain were inoculated. Roots were imaged 3- and 8-days post inoculation and seedlings were harvested at 8 days post inoculation.

2.5 Arabidopsis inoculation

Surface sterilized *A. thaliana* ecotype col-0 seeds were plated on ½ MS media, sealed with parafilm and placed in 4ºC for 72h. The plates were moved to climate chamber set to 22ºC light and 20ºC dark, 16 hours light and 8 hours dark, and grown for 6 days before inoculation. Two inoculation methods were tested: contact inoculation by root dipping and non-contact inoculation by dropping C. rosea spores at opposite end of the plate. For root dipping, seedlings were dipped in 10^6 spores/mL and transferred to fresh plates containing ½ MS media without sucrose. For non-contact inoculation, 100 µl of a 10^7 spores/mL spore solution was pipetted directly onto the media, at the side of the plate opposite from the seedlings. Both treatments used water instead of spore solution as control. 50 seedlings/strain were inoculated. All plates were placed in 22ºC day/20ºC dark, 16 hours light/8 hours dark conditions and plates were scanned 2- and 5-days post inoculation. Root length and lateral root count was measured in Fiji (https://imagej.net/software/fiji/). 7 days post inoculation seedlings were harvested and weighed before drying overnight in 50ºC and weighing again.
This experiment was repeated with the *A. thaliana* mutant containing the auxin reporter gene DR5-VENUS, using the non-contact method.

2.6 Metabolite bioassay

Strains were selected based on previous soil experiments with *C. rosea* and metabolite extracts were prepared and used for assessing antimicrobial effects of the *C. rosea*. The metabolite extracts were separated using HPLC (Appendix1) using ddH2O and acetonitrile as solvents. Fractions were stored at 4^{o}C until further use. To each well of a 96 well Microtiter plate (Sarstedt), 100 µl of metabolite extract was added and dried overnight in a laminar flow hood and then placed in a 37^{o}C incubator until completely dry. Liquid cultures of *P. syringae, E. coli* and *S. cerevisiae* were diluted to a concentration of 10^4 CFU/mL (0,1 OD_{600}) using liquid LB media. *B. cinerea* spores were diluted to 10^4 Spores/mL using PDB. To each well 100 µl of the microbe suspensions was added. Wells containing liquid media were used as control. For bacteria and yeast OD_{600} was measured every 4 hours and the plates were visually scored after the final measurement 36 hours after inoculation, comparing growth to control wells (Appendix 2). For *B. cinerea* OD_{600} was measured every 24 hours, and the plates were visually scored after the final measurement 6 days after inoculation. This experiment was repeated with *B. cinerea* using plates with 200 µl of metabolite extract.

2.7 Statistical analysis

All statistical analysis was done in R Studio (version 2026.01.0+392). For results of wheat inoculation (Fig 2, 3,4 & 5) and DR5-VENUS inoculation (Fig 8), one way ANOVA or Kruskall-Wallis test was used, depending on if data was normally distributed or not (Appendix 3&4). Post hoc analysis was done with TukeyHSD and Dunn's test respectively (Appendix 3&4). T.test was used for the results of the Arabidopsis trial inoculations (Fig 6). All tests used a 95% confidence interval.

3. Results

3.1 Wheat inoculation

3.1.1 Trial inoculation

Wheat seedlings inoculated with GR31 showed significantly longer roots than control (p=0.0099) four days post inoculation (dpi), however at 6dpi no significant differences compared to control was found (Fig 2C). There were no significant differences in the number of lateral roots between GR31 and control or 72E and control. Fresh and dry weight of roots and shoots were recorded and compiled to get seedling weight. The only significant difference was the fresh weight of roots inoculated with 72E (Fig 3C). Fresh root weight from 72E inoculated seedlings were significantly higher than control (p=0.0222) and GR3 (p=0.0145).

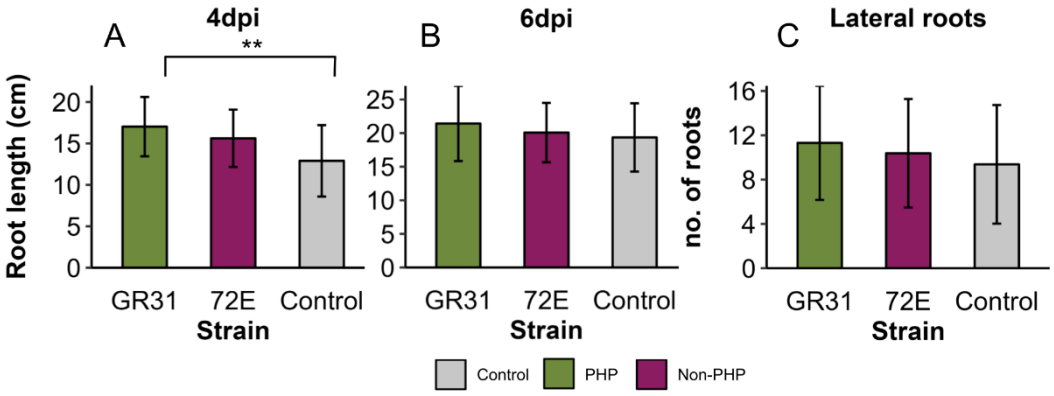

Figure 2: Results from trial wheat inoculation experiment. A-C shows Root length and lateral root number of inoculated plants. ***A****: 4dpi* ***B:*** *6dpi* ***C:*** *Lateral root number at 6dpi. Error bars show standard deviation. Asterisks indicate significant differences.* ** = *p < 0.01. GR31 inoculation resulted in significantly longer roots than control.*

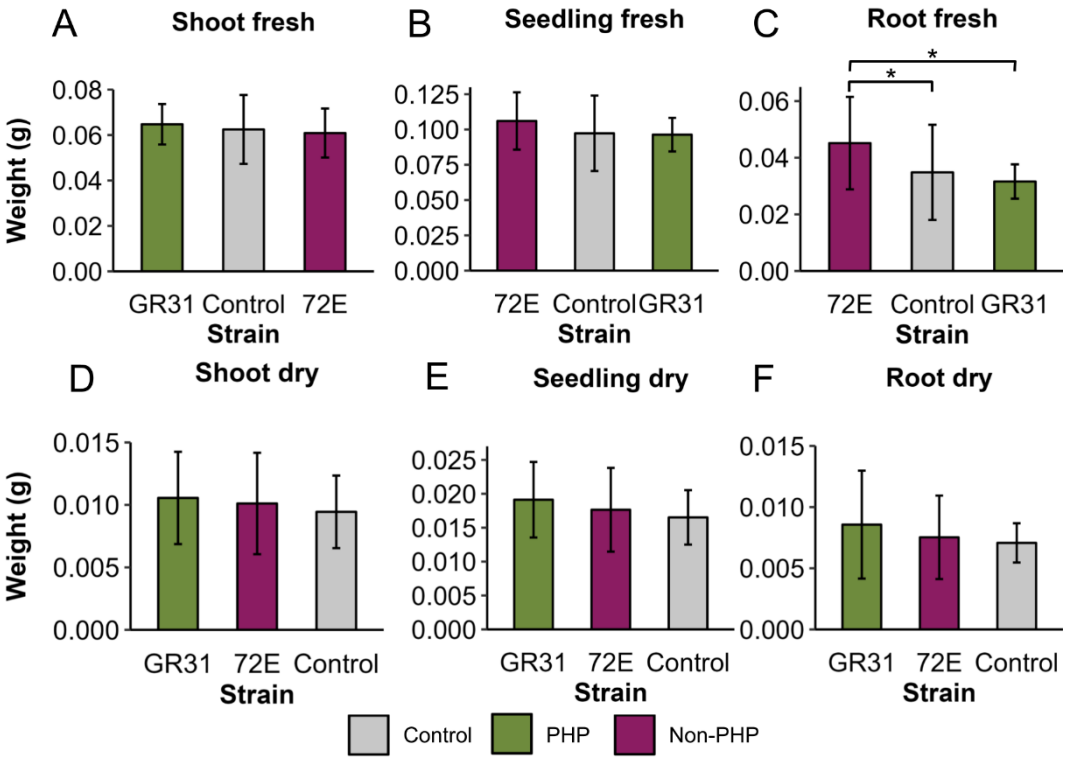

*Figure 3: Weight parameters of inoculated plants. **A-C**: Fresh weight **D-F**: Dry weight. Error bars show standard deviation. Asterisks indicate significant differences, * = $p < 0.05$. Only fresh root weight showed significant differences, 72E inoculation resulted in heavier roots than both control and GR31.*

3.1.2 Wheat inoculation using all strains

The inoculation was repeated using all 6 strains. Early on 1885 had longer roots than both GR31 ($p= 0.0025$) and 72E ($p=0.0070$), while GR31 had significantly shorter roots than control ($p=0.0411$). (Fig 4) These differences disappeared after 8 days. There were also no significant differences in lateral root number between the strains. 1885 resulted in significantly higher seedling fresh weight than control ($p=0.00194$) (Fig 5). All PHP strains had significantly higher shoot fresh weight than control and 1885 had significantly higher fresh weight than all non-PHP strains (Appendix 4). These differences were not present in dry weight for either seedling, shoot or root.

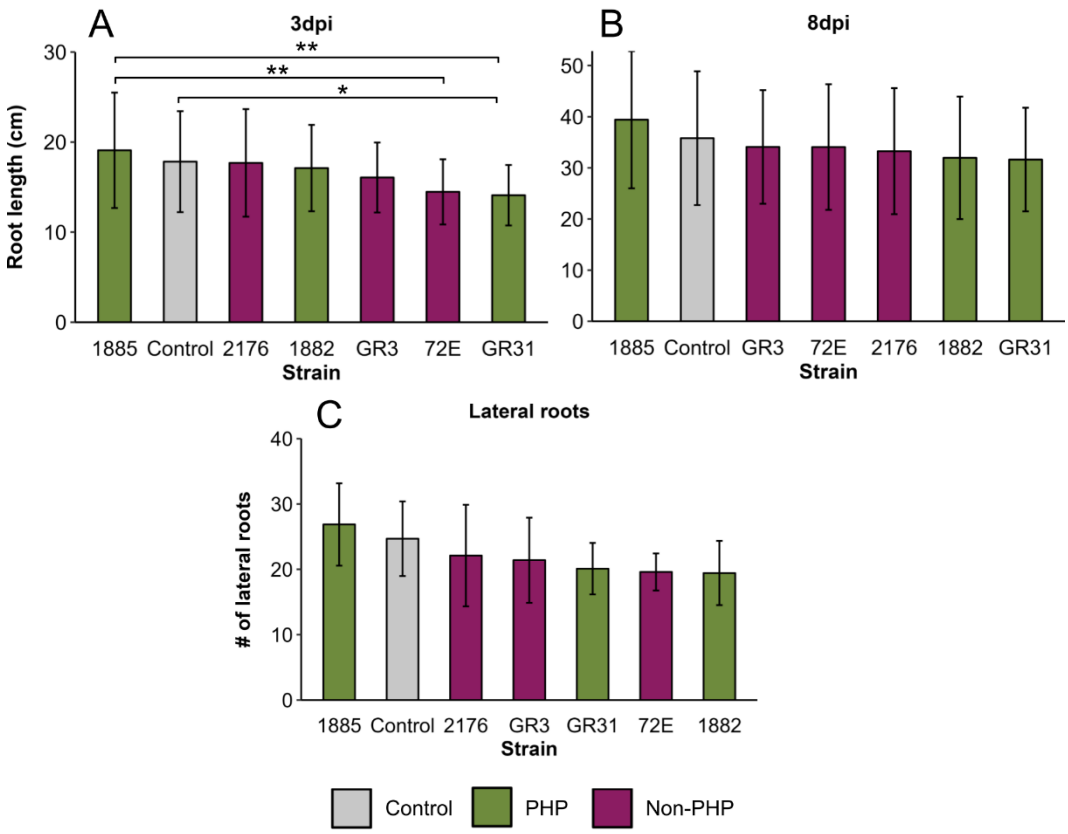

*Figure 4: Results of wheat inoculation using all strains. **A.** Root length 3dpi **B.** Root length 8 dpi **C**. Lateral root number. Error bars show standard deviation. Asterisks indicate significant differences, * = $p < 0.05$, ** = $p < 0.01$. After 3 days 1885 inoculated seedlings have significantly longer roots than 72E and GR31. GR31 inoculated seedlings had significantly shorter roots than control. After 8 days there were no significant differences between the strains. There were no significant differences in lateral root number.*

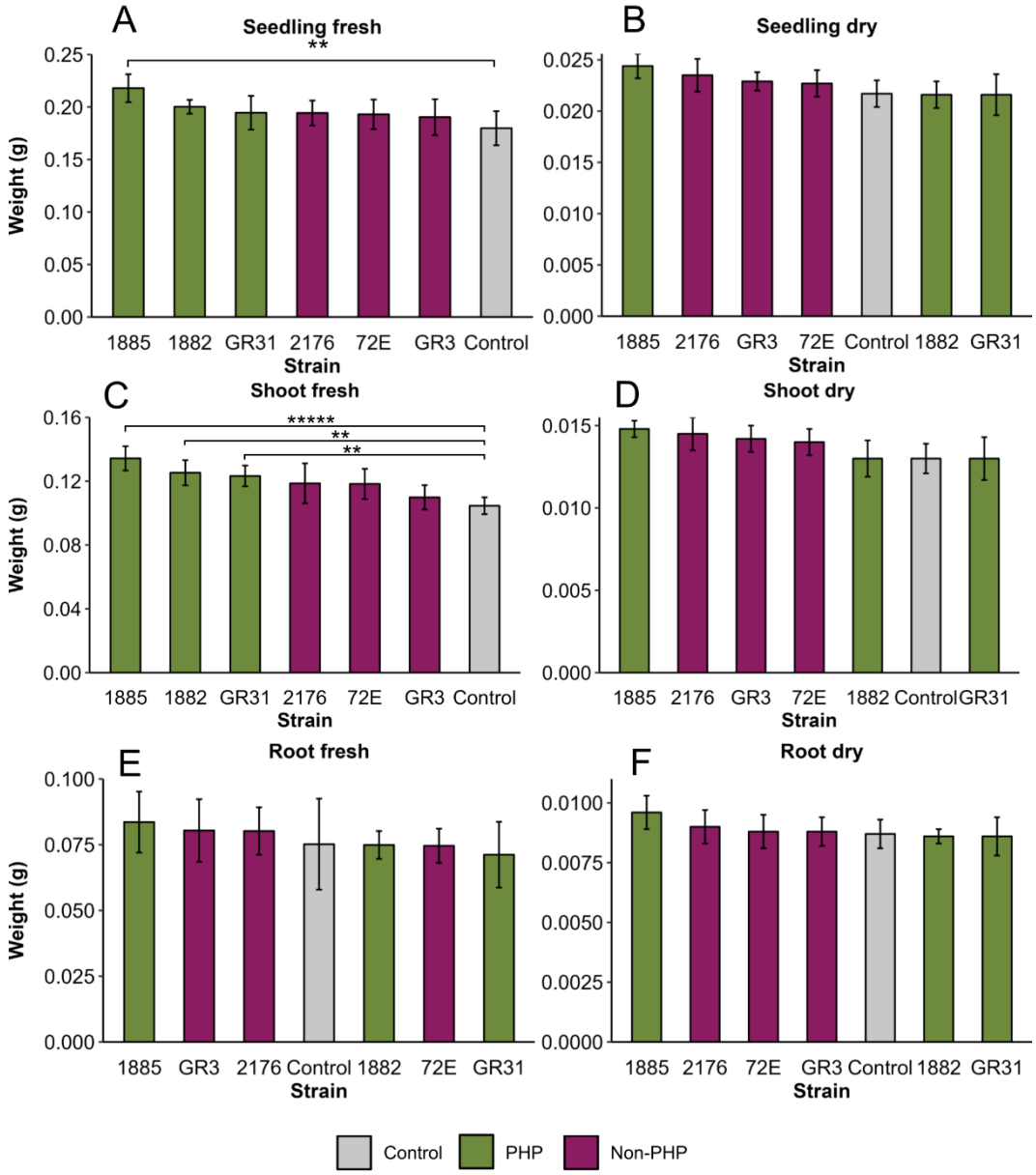

Figure 5: Results of wheat inoculation using all strains. ***A.*** *Seedling fresh weight* ***B.*** *Seedling dry weight* ***C****. Shoot fresh weight.* ***D.*** *Shoot dry weight* ***E.*** *Root fresh weight* ***F****. Root dry weight. Error bars show standard deviation. Asterisks indicate significant differences, ** = p <0.01, ***** = p < 0.00001. 1885 was the only strain that resulted in a significantly higher seedling fresh weight. All plant growth promoting strains had significantly higher shoot fresh weight than control.*

3.2 Arabidopsis inoculation

3.2.1 Trial experiment

A. thaliana seedlings were inoculated with strain GR31 using two different methods: root dipping and non-contact inoculation where fungal spores were added to the opposite side of the plate (Fig 7). Both inoculation methods resulted in plants with significantly reduced root length and lateral root number (Appendix 3) (Fig 6). Differences were observable after 5 days. Dipping resulted in plants with significantly lower fresh weight (p=0.0272). There were no differences in dry weight.

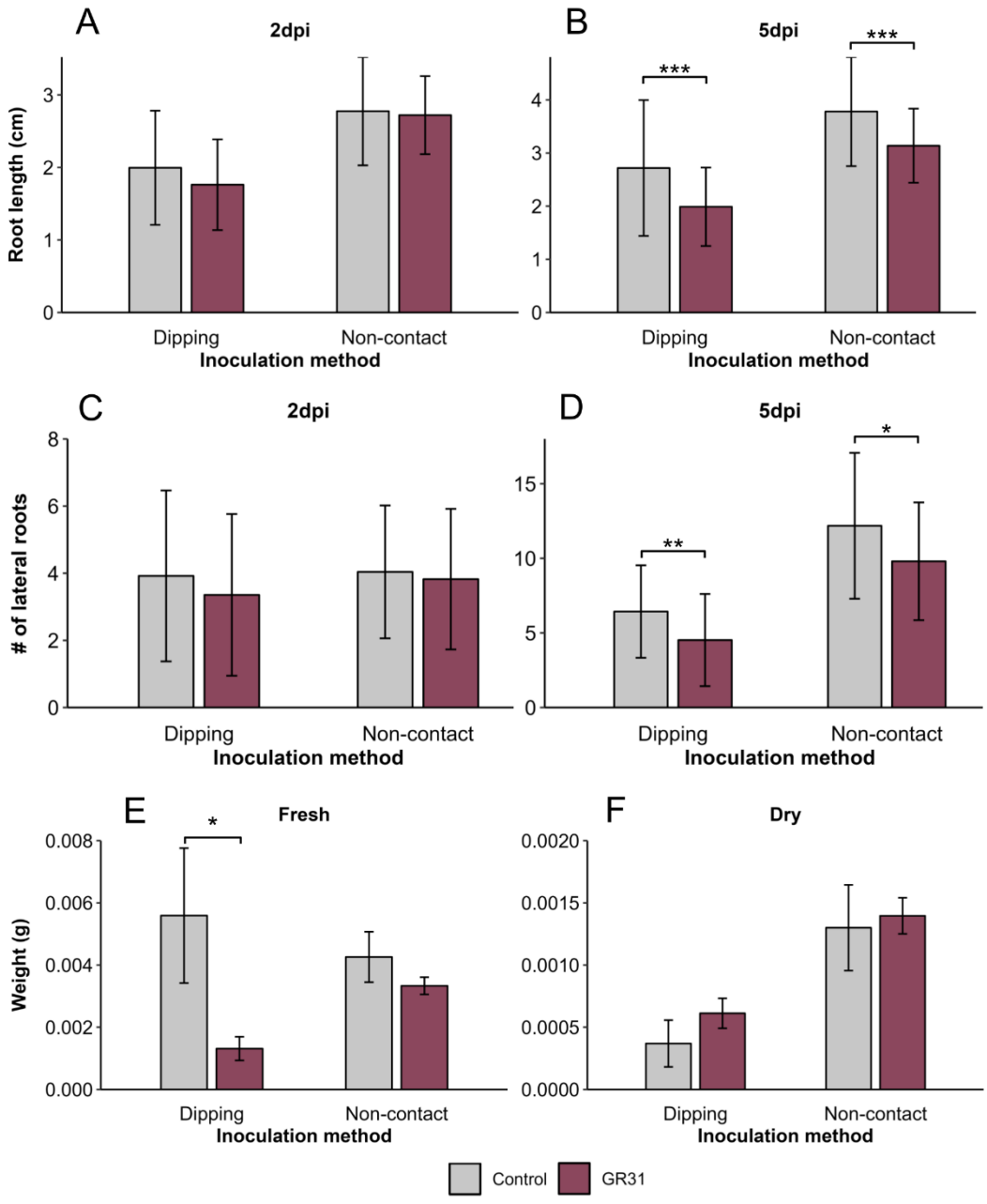

Figure 6: Results of GR31 inoculation of A. thaliana. ***A****: Root length 2dpi.* ***B****. Root length 5dpi.* ***C****. Lateral root number 2 dpi* ***D****. Lateral root number 5dpi.* ***E****. Fresh weight.* ***F****. Dry weight. Error bars show standard deviation. Asterisks indicate significant differences, * = p <0.05. After 5 days there was a significant difference in root length and lateral number for both inoculation methods. GR31 inoculation resulted in significantly shorter roots with fewer lateral roots. There was a significant difference in fresh weight for the Dipping method, with inoculated plants having reduced weight.*

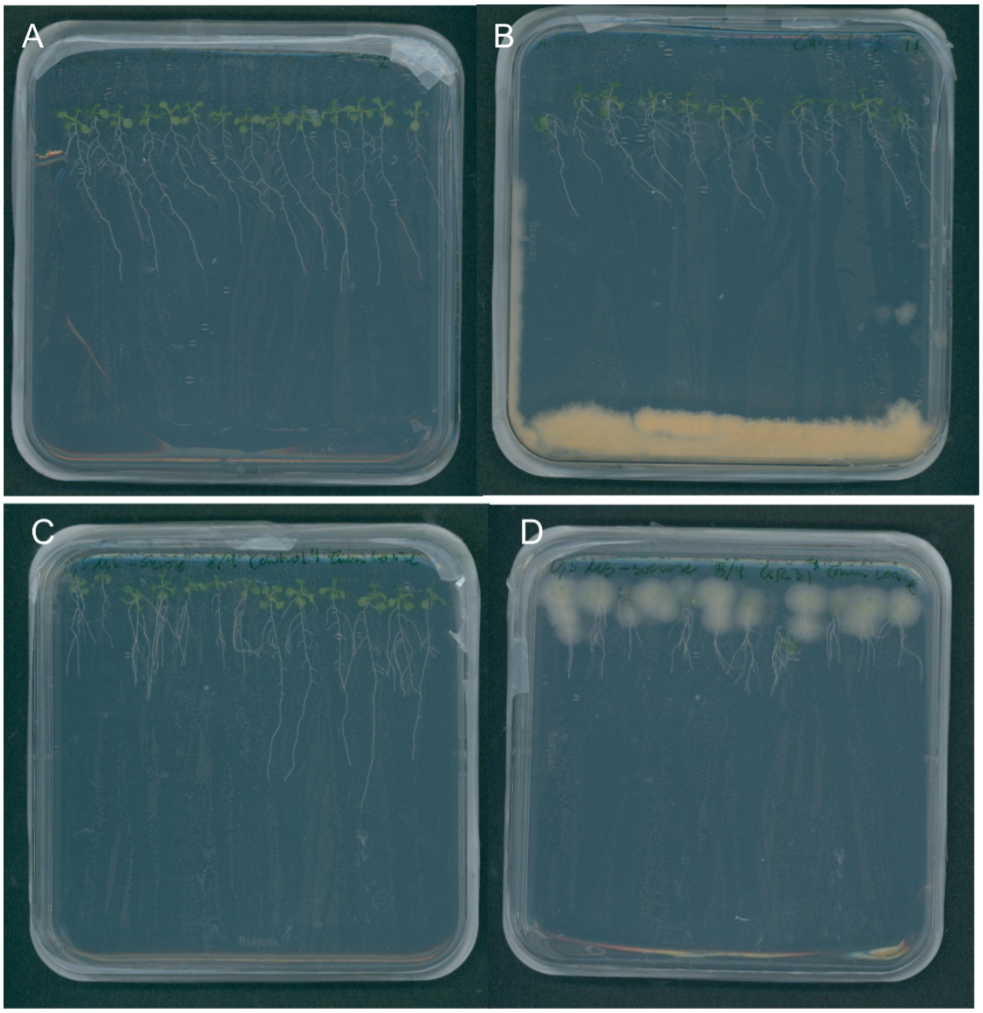

Figure 7: A. thaliana seedlings inoculated with GR31. Seedlings inoculated with root dipping were covered in fungal growth. ***A.*** *Control, root dipping* ***B.*** *GR31, root dipping* ***C.*** *Control, non-contact inoculation.* ***D.*** *GR31, non-contact inoculation.*

3.2.2 Auxin reporter inoculation

For the follow up experiment the *A. thaliana* mutant carrying the DR5-VENUS auxin reporter was inoculated using the non-contact method. After 2 days, plants inoculated with 72E had significantly longer roots than 1885 (p=0.0048) and 2176 (p=0.0173) and after 5 days 72E also had longer roots than GR31 (p=0.0072) (Fig 8). After 2 days 72E also had significantly more lateral roots than GR31

(p= 0.0325), this difference disappeared after 5 days. There were no differences in fresh or dry weight.

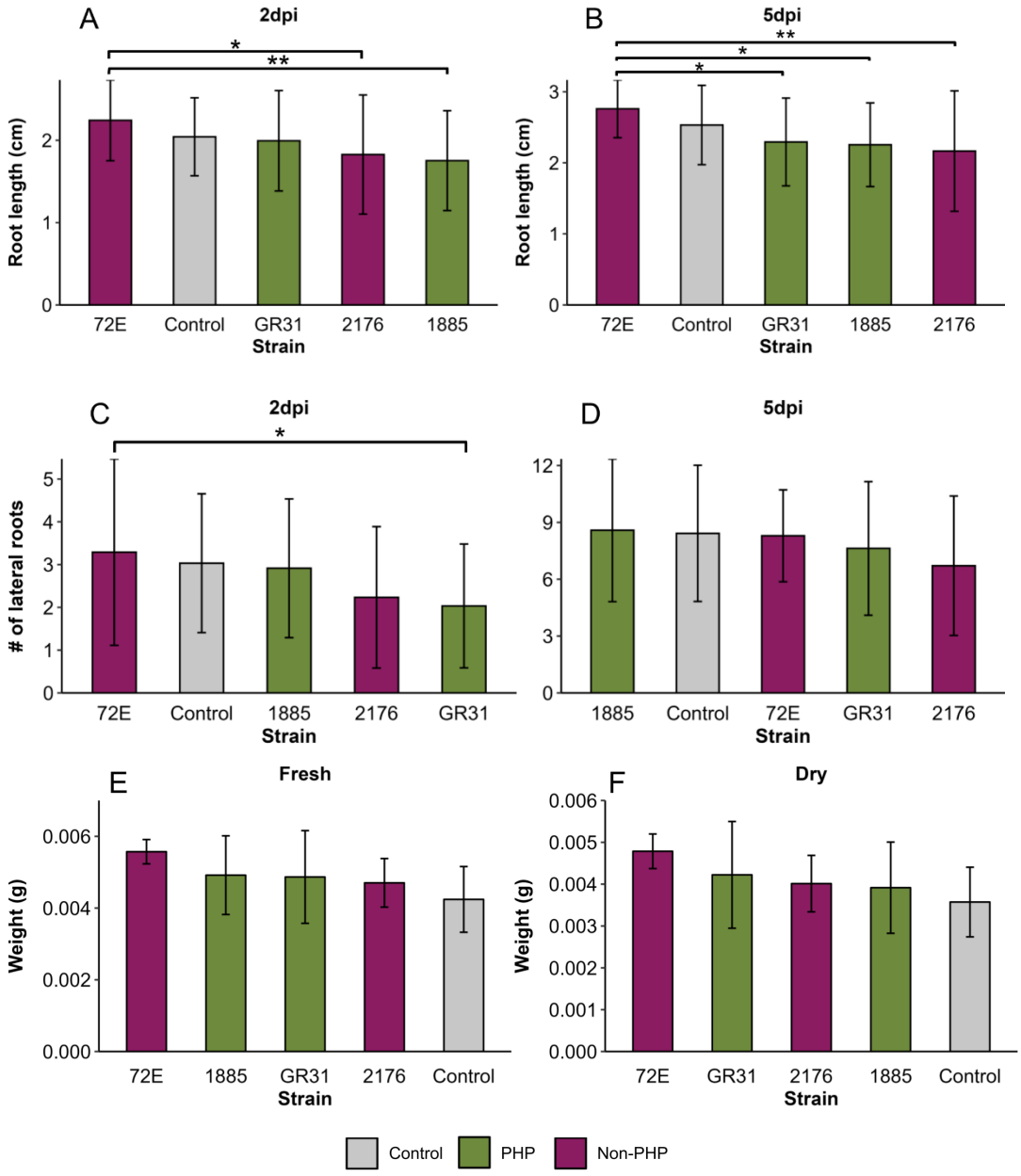

*Figure 8: Results of inoculation of A. thaliana mutant carrying DR5-VENUS auxin reporter. **A**: Root length 2dpi. **B**. Root length 5dpi. **C**. Lateral root number 2 dpi **D.** Lateral root number 5dpi. **E**. Fresh weight**. F**. Dry weight. Error bars show standard deviation. Asterisks indicate significant differences, * = p <0.05, ** = p <0.01. After 2 days 72E had significantly longer roots than 1885 and 2176 and after 5 days longer roots than GR31. After 2 days 72E had significantly more lateral roots than GR31 but after 5 days there were no significant differences between the strains. There were no significant differences in fresh or dry weight.*

Observing the inoculated *A. thaliana* seedlings under a fluorescence microscope shows a difference in YFP intensity (Fig. 9). GR31 (Fig. 9B) and 1885 (Fig. 9E) inoculated seedlings fluoresce brighter than control (Fig. 9A). 72E inoculated seedlings (Fig. 9F) show expression similar to control. 2176 seedlings were the only strain that showed varying expression, with certain seedlings emitting strong signals (Fig. 9C) and others showing very weak signals (Fig.9 D).

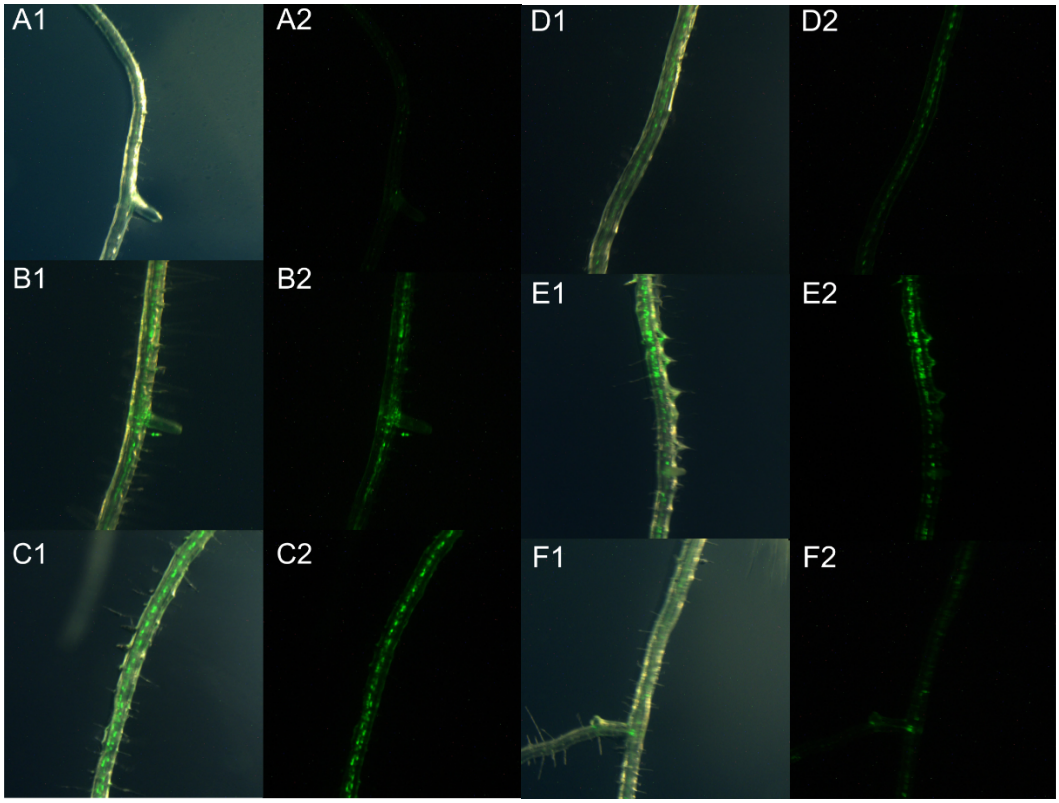

Figure 9: Fluorescence microscopy images of A. thaliana mutant carrying DR5-VENUS auxin reporter. Images representative of each strain. ***A.*** *Control* ***B.*** *GR31* ***C-D.*** *2176.* ***E.*** *1885.* ***F.*** *72E. PHP strains GR31 and 1885 showed increased fluorescence compared to control. 72E showed similar fluorescence to control. 2176 had varying fluorescence levels, higher in C than in D.*

3.3 Metabolite Bioassay

Bioassay using 96-well plates showed no differences in *S. cerevisiae* growth in any wells compared to control. This suggests no antimicrobial activity of secondary metabolite fractions towards *S. cerevisiae* (Fig 13*)*. For *E. coli*, wells that appeared to have inhibition upon visual inspection did not have OD_{600} values comparable to control (Fig 12). 2176 resulted in no growth of *P. syringae* in wells E4-E5, comparable to control wells H1-H3(Fig 10). For *P.syrinage,* fractions D1-G9 appear to have reduced growth compared to other fractions for all treatments (Fig 10). The repeated experiment with a higher concentration of metabolite against *B. cinerea* resulted in wells with no growth in all strains (Fig 11). While there were no wells that all 3 strains had in common a few overlapped between strains: C8 & G2 – 2176 and 1885, C5 – GR31 and 1885. *B. cinerea* did not have regions with slower growth as observed in *P. syringae.* There was no overlap in wells with antibacterial activity and antifungal activity.

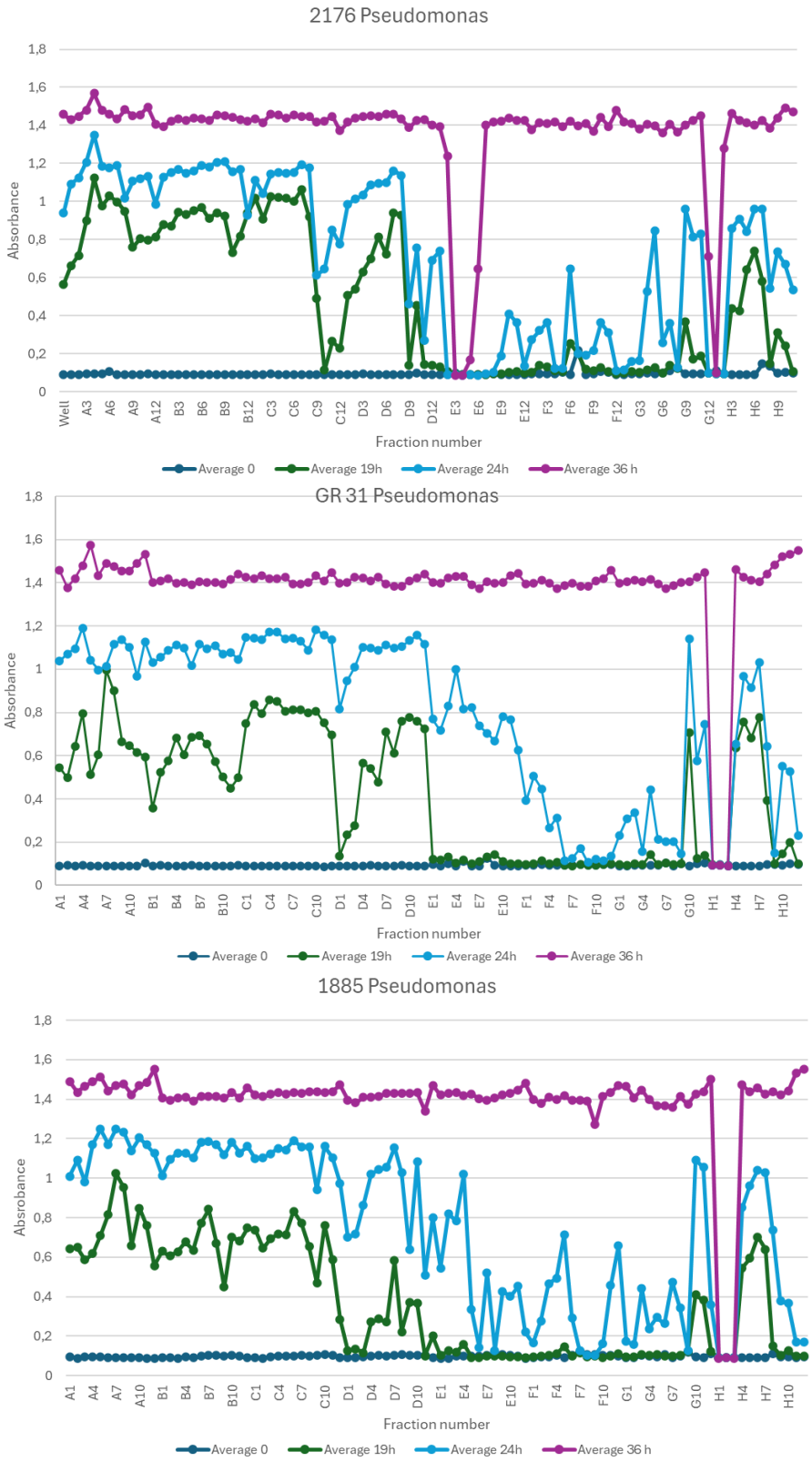

Figure 10: Absorbance measurements for metabolite bioassay on P. syringae. Metabolites from 2176 showed antimicrobial activity in wells E3-E5.

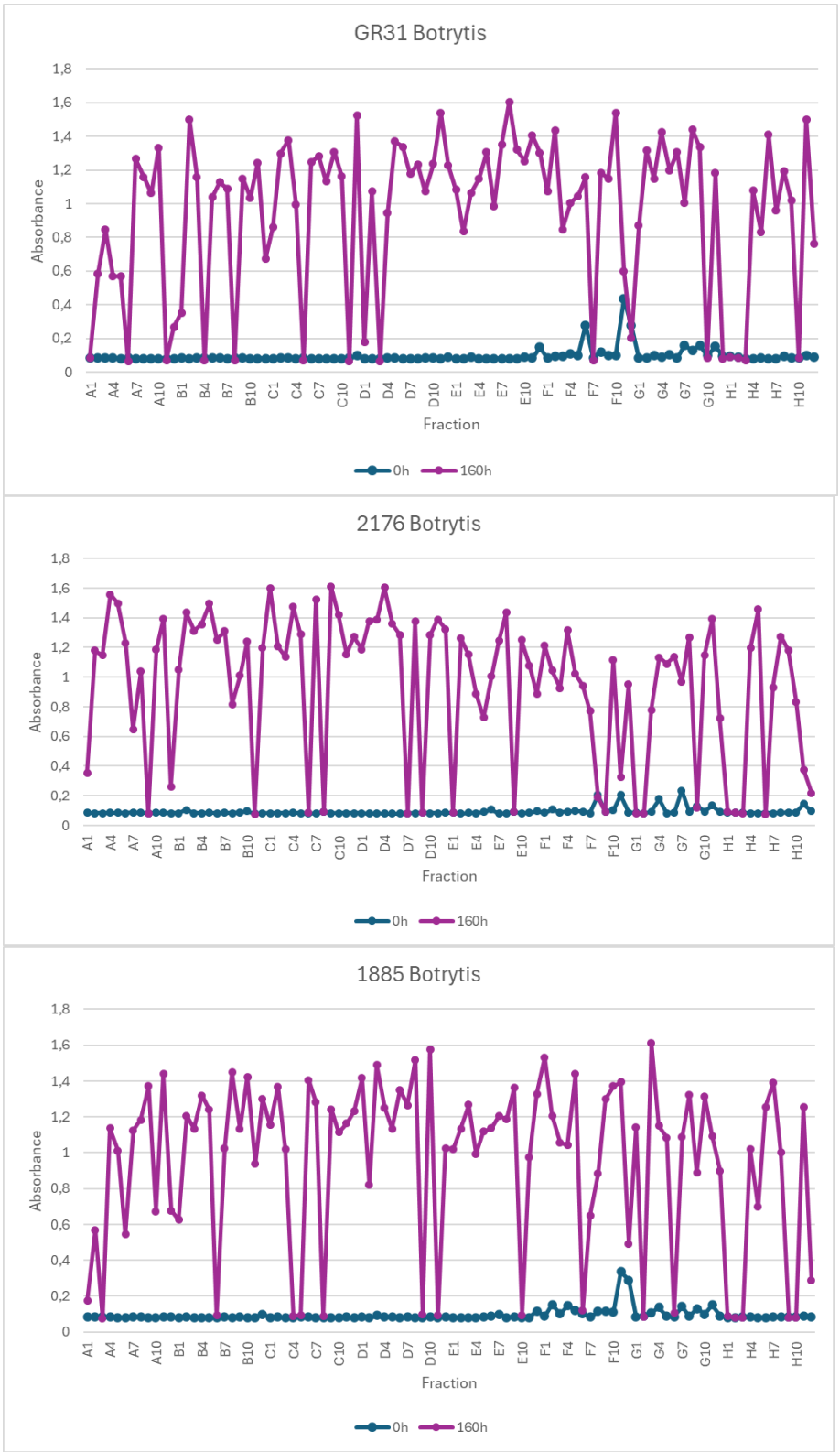

Figure 11: Absorbance measurements for metabolite bioassay on B. cinerea. Metabolites from all 3 strains showed antifungal activity. Few wells overlap between strains: C8 + G2 – 2176 & 1885, C5 – GR31 & 1885.

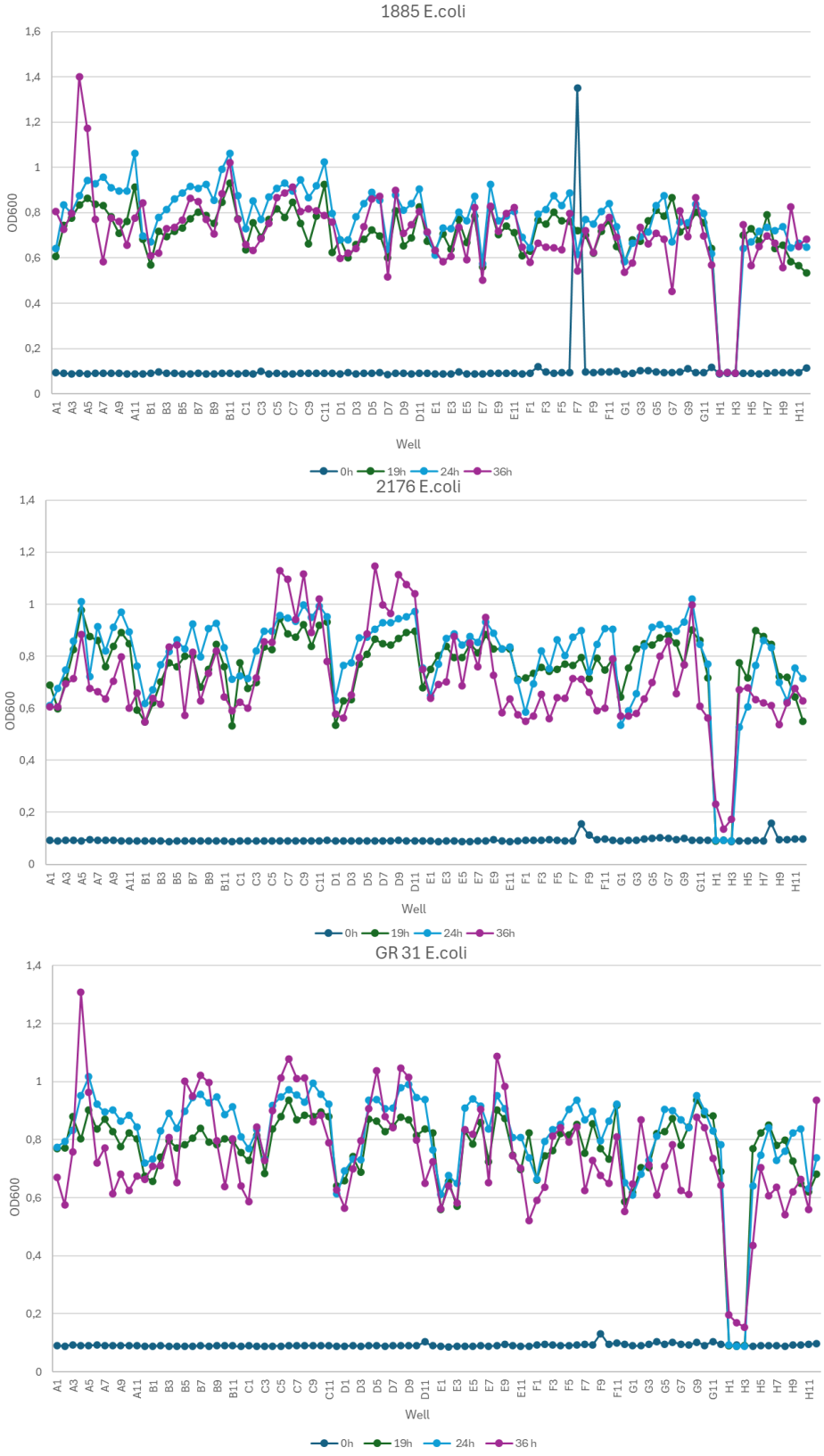

Figure 12: Absorbance measurements for metabolite bioassay on B. cinerea. OD values indicated no antibacterial activity comparable to control against E. coli.

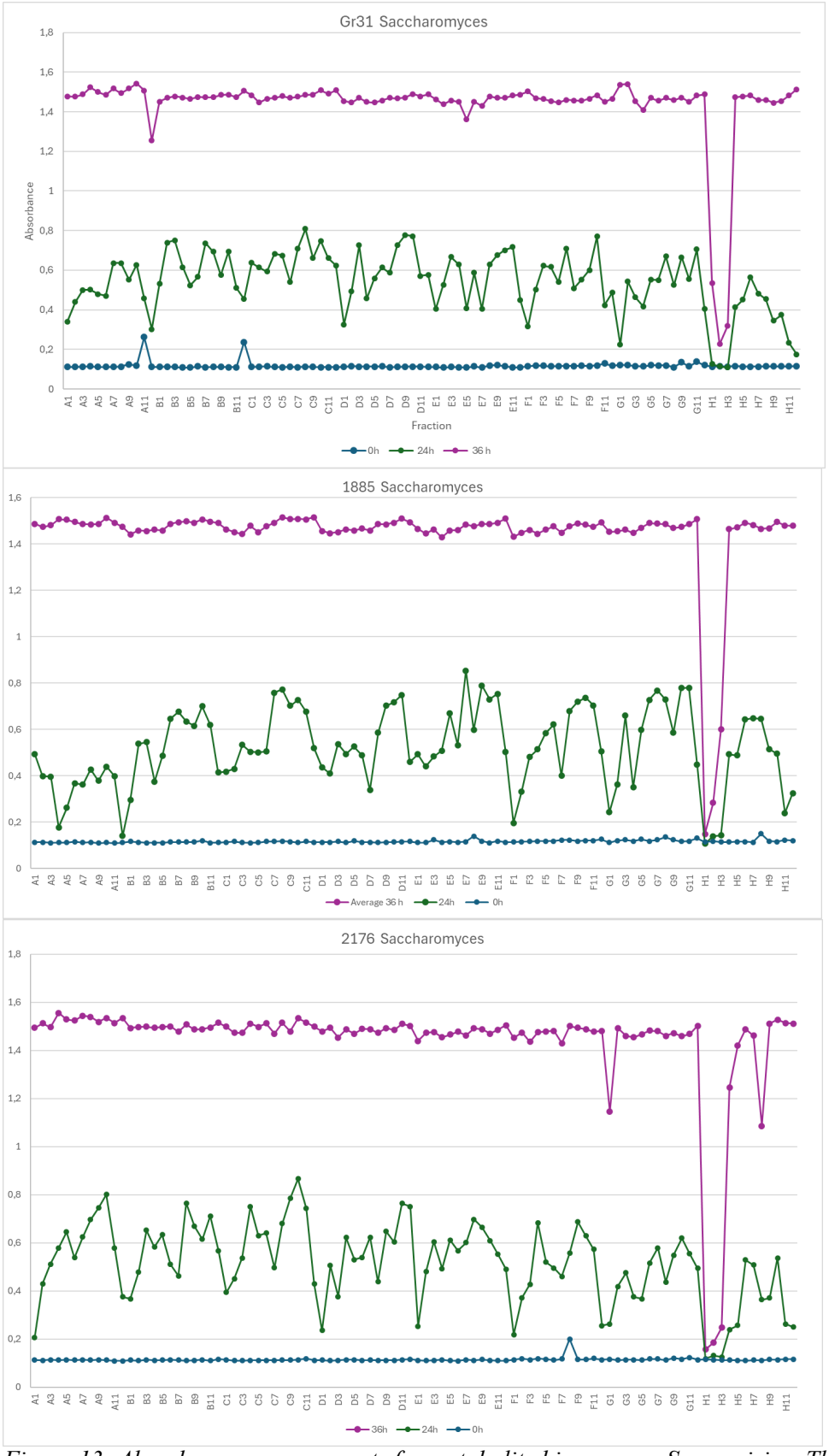

Figure 13: Absorbance measurements for metabolite bioassay on S. cerevisiae. There was no observed inhibition of growth and OD values indicated no antibacterial activity comparable to control.

4. Discussion

4.1 Wheat inoculation

In the trial experiment the assumption was that the seedlings did not get adequate light as they were grown in the dark after inoculation and that the roots did not make contact with the growth media. Initially we believed that they did not grow enough to be able to observe these differences properly. However, when we repeated the experiment using all strains and improved growth conditions we saw the same results. An initial hypothesis was that growth promotion is partially due to an alteration of root architecture where the seedlings develop longer roots with more lateral roots, which would increase the surface area and thus the plants' ability to take up nutrients and water. This is partially based on transcriptomic data from the study where the PHP/non-PHP classification is from (unpublished) but also consistent with recorded PHP effects from *C. rosea* (Chen et al. 2024; Wu et al. 2026). These results indicate that the PHP-effect seen in wheat is not caused by promoting growth of roots. Notably the PHP strains all increased shoot fresh weight and 1885 also increased seedling fresh weight, a difference not observed in the dry weight i.e. biomass. This is however consistent with previous findings, as many reports of *C. rosea* increasing biomass either only recorded fresh weight (Chen et al. 2024) or only saw an increase in fresh weight with no difference in dry weight even though plants were visibly more vigorous (Wu et al. 2026). This could indicate that PHP inoculation leads to higher moisture content in the shoot.

The PHP/non-PHP classification was based on soil experiments, meaning these effects might not translate fully to *in vitro* experiments. A sterile environment will not show indirect effects, for example growth promotion caused by outcompeting other microorganisms. The soil experiments were also done over a longer time, and a shorter in vitro experiment might not show the effects seen after weeks in only a few days of growth. There are however some observations that can be made. For 'Happy' it seems that 1885 is the best PHP-strain as it consistently results in the highest values across all measurements (Fig 4, 5). It is also important to note that the PHP-strains do not always group together, in the follow up experiment we see GR31 quite consistently has the lowest values, lower than the non-PHP strains (Fig 5). This could be an effect of genotype x genotype interactions, where whether we see beneficial effects depends on the combination of fungal strain and plant genotype. While these differences are not always significant, it is an interesting trend.

Building on these results it would be interesting to see if there is a PHP-effect in the presence of pathogens. This could be done by co-inoculation of wheat by *C. rosea* and other pathogens, for example *B. cinerea* or *F. graminearum*, two species we know that *C. rosea* can control. This would confirm the hypothesis that growth promotion of wheat is an indirect interaction. This could also be confirmed by comparing gene expression of hormone biomarkers, ex auxin, using RNA extraction and qPCR, comparing gene expression of inoculated/non-inoculated wheat seedlings. If there aren't any significant changes in expression that would further confirm that this is an indirect interaction.

4.2 Arabidopsis inoculation

Contrary to the wheat, significant effects on root length were observable in the later timepoints and the no-PHP strain 72E outperformed the PHP strains in root length. In the follow up we can also see that for most measurements 72E now has the highest values, compared to 1885 in the wheat inoculation. This suggests that the PHP/non-PHP-classification that was based on experiments in wheat does not hold true for *A. thaliana* and strengthens the hypothesis that there are genotype x genotype effects when *C. rosea* interacts with plants. When comparing the fluorescence of the different strains we can see that PHP-strains 1885 and GR31 show a strong green signal throughout the root, compared to the very weak signal from control. We also see that 72E shows a weaker signal than the PHP strains. 2176 had more variation in YFP intensity than the other strains, with some plants fluorescing brightly (Fig 8C2) and some much weaker (Fig 8D2). These observations would be strengthened by fluorescence quantification, giving values we could compare statistically. This would also require a larger sample size of photos. Nevertheless, the observations suggest that there could be a difference in hormone expression.

These results suggest that in *A. thaliana* a stronger auxin induction by *C. rosea* leads to inhibition of root growth. This could be the case, as we know from other studies that growth promotion without physical contact – in the form of VOCs – has a dose dependent relationship where too high concentrations lead to inhibition of growth (Kottb et al. 2015). It does however raise some questions, since with an increase in auxin levels we expect an increased growth rather than inhibition. There is some evidence that wheat exposed to high concentrations of synthetic auxin have reduced growth (Lyubushkina et al. 2025), suggesting that similar to VOCs, beneficial auxin effects could have a dose-dependent relationship.

The cause of this inhibition could be investigated by reducing the concentration of inoculum and observing if these effects remain or if lower concentrations lead to growth promotion. This would also reveal if the non-PHP strains had PHP-effects

on *A. thaliana.* Continuing based on these results it would be interesting to look at all strains to see if the trend continues: do all PHP strains reduce growth in A. thaliana? This could be complemented by comparing different concentrations of inoculum to note any dose dependent effects. Differences in auxin expression could also be confirmed using RNA extraction and RT-qPCR of auxin genes, to determine if the inoculation upregulates the expression of these genes.

4.3 Bioassay

When visually scoring the plates (Appendix 2) there were a few wells in the *E. coli* bioassay that looked like they showed inhibition. This was however not confirmed by the OD measurements. Looking at all metabolic activity regardless of species it is interesting to note that the fractions showing inhibition on *P. syringae* did not overlap with the fractions that showed inhibitory activity on *B. cinerea.* Considering that fungi and bacteria are structurally different, for example varying in membrane composition and permeability, it is plausible that they have different sensitivity towards these metabolites. Fractions showing activity towards *B. cinerea* varied between strains with only a few overlaps, none shared by all 3 strains. These results show that the strains most likely produce different metabolites and that there is strain-to strain variation in antimicrobial activity. Interestingly none of the strains produced metabolites with inhibitory effects on *S. cerevisiae.*

Identifying which compounds are present in the fractions of interest would most likely clarify the differences between strains that we observe. The bioassay could also use further optimization for antibacterial activity, as for *E. coli* the growth does not change after the first timepoint. This suggests they have already grown as much as the media allows and observing them earlier could reveal if growth was slowed, similar to what we see in *P. syringae.*

5. Conclusion

The aim of this project was to investigate how *C. rosea* promotes plant growth in wheat and trying to determine whether it is a direct or indirect interaction between the fungus and plant. To further investigate the mechanism, the interaction was also investigated in the model plant *A. thaliana*. These results suggest that in wheat this is not a direct interaction between the plant and fungus but rather a result of indirect interactions, protecting the plant from pathogens through its mycoparasitic and antibiotic abilities. In *A. thaliana* you could interpret the results as a more direct interaction, as the different strains did affect the levels of auxin in the root and result in changes in root architecture. Furthermore, these results confirm what we already know: *C. rosea's* PHP-effects are strain-specific and plant genotype specific. This is most clearly exemplified by the difference in effect of PHP-strains on *A. thaliana* and wheat. A non-PHP strain in wheat is better than PHP strains in *A. thaliana*. A better understanding of the mechanisms behind *C. rosea's* PHP-effects will help us utilise the full potential of this fungus, helping us to achieve our agricultural goals in a sustainable way and reap more than what we sow.

6. Acknowledgements

First and foremost, I want to thank my supervisors Mukesh Dubey and Magnus Karlsson for their invaluable guidance and help throughout this project. Thank you for answering my many, many, questions and for always being ready to help. Thank you to Ke Zhang, Anders Broberg, Jonathan Cope and Noe Adrien for all your practical help and instructions, I learned a lot from you. Thank you to everyone at the Department of Forest Mycology and Plant Pathology for welcoming me, you made these months a wonderful experience. Thank you to Georgios Tzelepis, Agnes de Val and Deimante Kasparaviciute for your feedback, for helping me to make this text the best it could be.

7. Popular scientific summary

We can increase our yield by protecting our crops from pathogens and trying to optimise their growth conditions. One way to get both benefits is to use biological control agents: a living organism that reduces negative effects on the plants by pathogens or pests. They work as a more sustainable alternative to traditional chemical pesticides. Some of these biocontrol agents also have plant growth promoting effects, like for example the fungus *Clonostachys rosea*. While we do know that it has these growth promoting effects, we still don't know how it works. There are two main options: the fungus reduces pathogens in the soil and thus protects the plant from harm, or the fungus directly interacts with the plant by secreting something that makes it grow better. In this project we wanted to figure out which of these mechanisms were the cause of growth promotion in wheat. We compared six strains, three with known growth promoting abilities and three with no effect on growth promotion to try and find differences between the strains that could explain this phenomenon. The main experiments involved dipping the roots of wheat and the model plant *Arabidopsis thaliana* in *C. rosea* spore solutions and observing their growth over time. We were looking for any changes in root architecture like root length and root branching, under the assumption that longer and more branched roots would lead to better nutrient and water uptake. We thought this could be one way that *C. rosea* improves growth. We also conducted a metabolite bioassay, where metabolites from *C. rosea* were extracted and tested for antimicrobial activity. This would show differences in the strains ability to reduce pathogen growth.

We found that – as it often is in biology – it depends! Experiments with wheat showed no lasting effects on root growth and no increases in biomass. On the other hand, experiments in the model plant *Arabidopsis thaliana* showed that inoculation generally reduced growth and caused lasting changes in the root architecture. In *A. thaliana* we saw that this growth reduction happened without physical contact between the fungus and plant, suggesting it secretes something that changes the growth of the plant. We repeated this experiment with a genetically modified *A. thaliana* containing a plant growth hormone reporter, making differences in hormone expression observable with fluorescence microscopy. We did see a visual difference between the strains, indicating that the regulation in Arabidopsis is caused by hormonal changes. In the bioassay, all strains had compounds that could inhibit microbial growth, suggesting that they possess the ability to indirectly promote growth through reducing pathogen presence in the soil. Our results confirm what we already know, the growth promotion effects of *C. rosea* are highly strain and species specific and further investigation is needed to find optimal combinations of strain and plant cultivar to reap more than what we sow.

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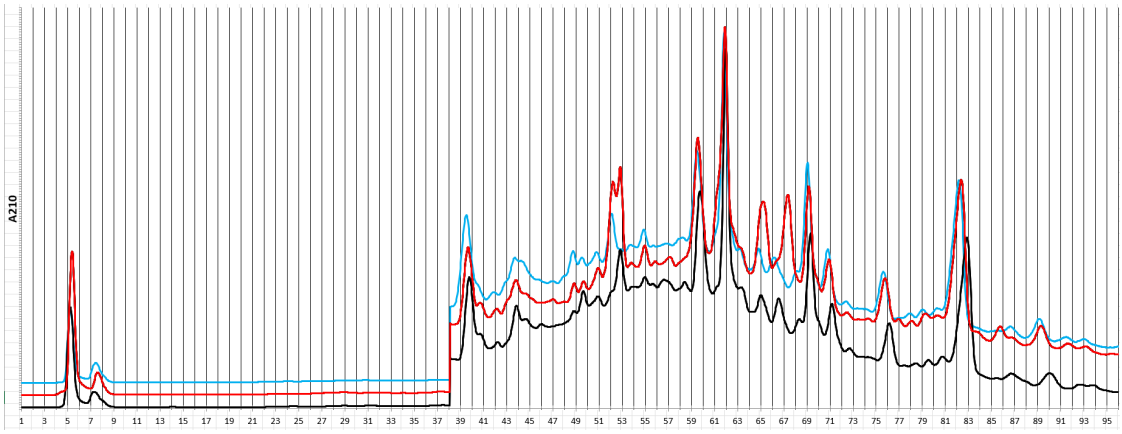
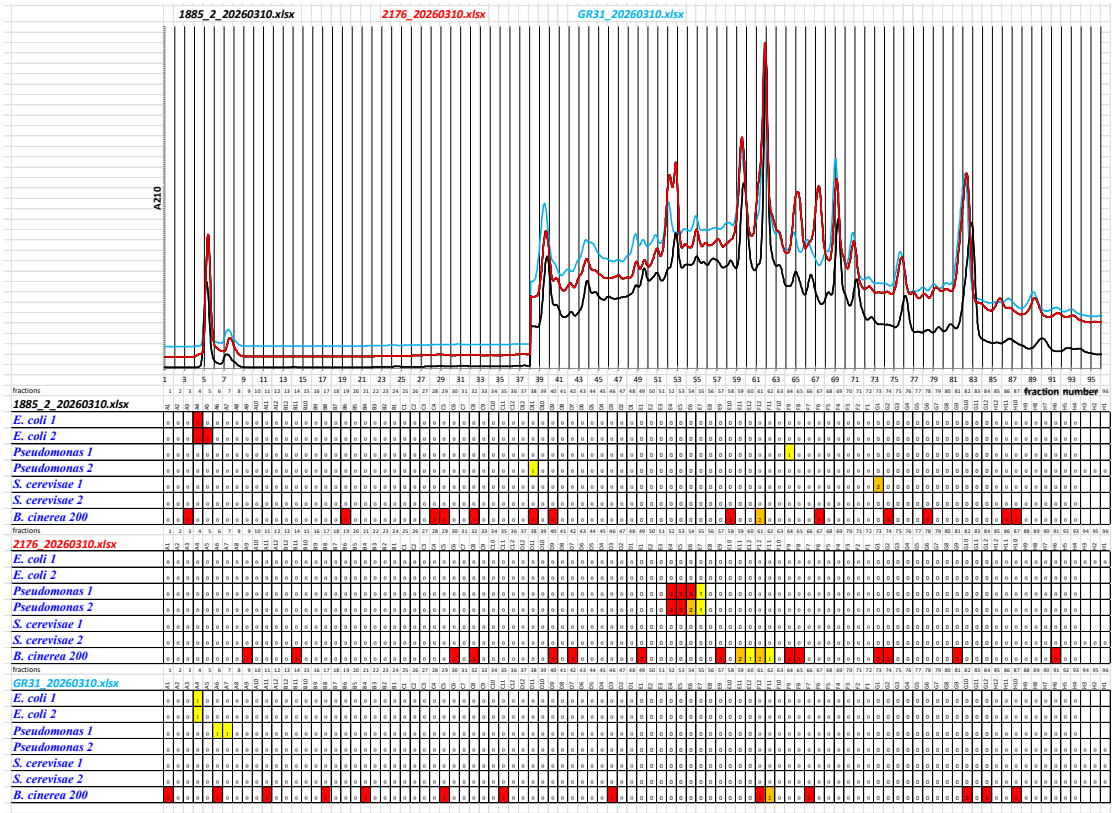
Appendix



A1: LC chromatogram from the separation of metabolites. Black: 1885, Red: 2176, Blue: GR3. Y-axis shows absorbance, X-axis shows fraction number.



A2: LC chromatogram with the visual scoring. Wells were scored compared to control, from 0: no inhibition (white) to 3: Complete inhibition (red).

A3.Table of statistical tests performed. Significant p-values in bold

Experiment	Mesurement	Test	p-value	Post hoc
Arabidopsis trial dip	Root length 2dpi	t.test	0,1057	
	Root length 5dpi	t.test	**0,0007464**	
	Lateral roots 2dpi	t.test	0,2612	
	Lateral roots 5dpi	t.test	**0,002769**	
	Fresh weight	t.test	**0,02715**	
	Dry weight	t.test	0,6787	
Arabidopsis trial non-contact	Root length 2dpi	t.test	0,7521	
	Root length 5dpi	t.test	**0,0006127**	
	Lateral roots 2dpi	t.test	0,5277	
	Lateral roots 5dpi	t.test	**0,01513**	
	Fresh weight	t.test	0,1031	
	Dry weight	t.test	0,6183	
Venus	Root length 2dpi	Kruskall	**0,0106**	Dunn
	Lateral roots 2dpi	Kruskall	**0,01335**	Dunn
	Root length 5dpi	Kruskall	**0,001947**	Dunn
	Lateral roots 5dpi	Anova	0,187	
	Fresh weight	Kruskall	0,2938	
	Dry weight	Kruskall	0,2835	
Wheat trial	Root length 4dpi	Anova	**0,0121**	TukeyHSD
	Root length 6dpi	Anova	0,6456	
	Lateral roots	Anova	0,57	
	Seedling fresh	anova	0,348	
	Seedling dry	Kruskall	0,3022	
	Shoot fresh	Anova	0,656	
	Shoot dry	Kruskall	0,7804	
	Root fresh	Kruskall	**0,006487**	Dunn
	Root dry	Kruskall	0,4407	
Wheat repeat	Root length 3dpi	Anova	**0,00056**	TukeyHSD
	Root length 8dpi	Anova	0,198	
	Lateral roots	Anova	0,301	
	Seedling fresh	Anova	**0,00833**	TukeyHSD
	Seedling dry	Anova	**0,0249**	TukeyHSD

	Shoot fresh	Anova	**5,7e-06**	TukeyHSD
	Shoot dry	Anova	**0,00967**	TukeyHSD
	Root fresh	Anova	0,648	
	Root dry	Anova	0,226	

A4. Table of post hoc analysis performed, p-value column shows groups with significant differences. Note that Wheat repeat, seedling dry and shoot dry do not show significant p-values even if the results of the test in table 3 was significant.

Experiment	**Mesurement**	**Post hoc**	**p-values**
Venus	Root length 2dpi	Dunn	**72E-2176:** 0,0173 **72E-1885:** 0,0048
	Lateral roots 2dpi	Dunn	**GR31-72E:** 0,0325
	Root length 5dpi	Dunn	**72E-2176:** 0,0045 **72E-1885:** 0,0036 **72E-GR31:** 0,0072
Wheat trial	Root length 2dpi	TukeyHSD	**GR31-Control:** 0,0099
	Root fresh	Dunn	**72E-Control:** 0,0222 **72E-GR31** 0,0145
Wheat repeat	Root length 3dpi	TukeyHSD	**GR31-Control**: 0.0411 **GR31-1885:** 0.0025 **72E-1885:** 0.0070
	Seedling fresh	TukeyHSD	**Control-1885:** 0.0019
	Seedling dry	TukeyHSD	**Control-1885:** 0.0607
	Shoot fresh	TukeyHSD	**Control-1882:** 0.0012 **GR3-1882:** 0.0352 **2176-1885:** 0.00267 **72E-1885:** 0.0262 **Control-1885:** 0.0000049 **Gr3-1885:** 0.0002 **GR31-Control:** 0.0039
	Shoot dry	TukeyHSD	**Control-1885:** 0.0584 **1885-1882**: 0.0598

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