Dynamics of the Soil Microbiome in Ginseng Gardens

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A thesis submitted in partial fulfillment of the requirements for the Master of Science degree in Biology
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Abstract

Ginseng Replant Disease (GRD) is a syndrome in which ginseng cannot be cultivated in soil previously used to grow ginseng. Since GRD can persist for decades, it severely impacts the Ontario ginseng industry. To better understand the origin of GRD, the impact of ginseng cultivation on the soil microbiome was investigated in bulk soil of three newly planted ginseng gardens in Ontario, from seeding through two years of cultivation. While specific trends in species richness, diversity and composition were unclear, PERMANOVA analyses confirmed that they changed over time. Known GRD-related pathogens, including *Ilyonectria mors-panacis* and *Fusarium oxysporum*, were detected in ginseng garden soils. An increase in the relative pathogen load in the soil of ginseng gardens may be a primary driver of the development of GRD but could also serve in the development of a diagnostic tool to identify risk of GRD in soils of unknown ginseng cultivation history.

Keywords

Ginseng, Ginseng Replant Disease, GRD, microbiome, mycobiome, monoculture, NGS, metabarcoding
Summary for Lay Audience

Ginseng is a plant farmed in Ontario for its roots, which are used in traditional Chinese medicine, vitamins, food, and drinks for its health benefits. Ginseng Replant Disease (GRD) is a disease that causes ginseng to grow poorly in soil that has previously been used to grow ginseng. GRD causes fewer, and smaller, roots to grow and increases the amount of root rot. GRD can last for decades and has greatly decreased the amount of land still available for ginseng farming in Ontario, which threatens the Canadian ginseng industry. While the exact cause of GRD is unclear, previous research has identified fungal pathogens that are present in most GRD-diseased gardens. Studies in Asia have found a decrease in the number and abundance of bacterial species and an increase in the number and abundance of fungal species in GRD soil. In this project, I sequenced fungal DNA found in ginseng garden soil from three newly planted ginseng gardens from seeding through two years of growth. The number and identity of microorganisms in soil influences the health of the soil, which then affects the health of the plants. By sampling four times a year, a more precise study of the changes in the fungi present in ginseng garden soil was achieved.

While I found that there are changes in fungal composition occurring in the soil, the changes were not large and were difficult to precisely define. I propose the two-year duration of ginseng cultivation in the study gardens was not long enough to influence the soil microbes. However, ginseng pathogens were found in my samples in low abundance which means there is an opportunity for these pathogens to increase in abundance over time, and potentially cause GRD symptoms in these gardens after harvest.
Acknowledgments

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I would like to dedicate my thesis to my late grandfather who passed away halfway through my degree. He always asked me about my project and bragged endlessly to all his friends about his granddaughter, “Dr. Dirt”. I wish he could be here with me to celebrate the completion of my work, but I know he will be looking down on me with adoration and pride.
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<th>Description</th>
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<tbody>
<tr>
<td>ANOSIM</td>
<td>Analysis of similarities</td>
</tr>
<tr>
<td>ANOVA</td>
<td>Analysis of variance</td>
</tr>
<tr>
<td>BLASTn</td>
<td>Basic local alignment search tool - nucleotide</td>
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<tr>
<td>COX</td>
<td>Cytochrome c oxidase</td>
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<tr>
<td>DNA</td>
<td>Deoxyribonucleic acid</td>
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<tr>
<td>GRD</td>
<td>Ginseng replant disease</td>
</tr>
<tr>
<td>HIS3</td>
<td>Histone 3</td>
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<tr>
<td>ITS</td>
<td>Internal transcribed spacer</td>
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<tr>
<td>NGS</td>
<td>Next generation sequencing</td>
</tr>
<tr>
<td>OGGA</td>
<td>Ontario Ginseng Growers Association</td>
</tr>
<tr>
<td>OMAFRA</td>
<td>Ontario Ministry of Agriculture, Food and Rural Affairs</td>
</tr>
<tr>
<td>OTU</td>
<td>Operational taxonomic unit</td>
</tr>
<tr>
<td>PCoA</td>
<td>Principal coordinate analysis</td>
</tr>
<tr>
<td>PCR</td>
<td>Polymerase chain reaction</td>
</tr>
<tr>
<td>PERMANOVA</td>
<td>Permutational multivariate analysis of variance</td>
</tr>
<tr>
<td>QIIME2</td>
<td>Quantitative Insights in Microbial Ecology version 2</td>
</tr>
<tr>
<td>RNA</td>
<td>Ribosomal deoxyribonucleic acid</td>
</tr>
<tr>
<td>TEF1</td>
<td>Translation elongation factor 1</td>
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1. Introduction

1.1 Ginseng

Ginseng (Panax spp.) species are herbaceous perennial plants in the family Araliaceae (Wen & Zimmer, 1996; Kim et al., 2017). There are many species of Panax, but the most commonly cultivated ones for human use include Panax ginseng (Korean or Asian ginseng), P. quinquefolius (American ginseng) and P. notoginseng (Chinese notoginseng or Sanchi) (Lu et al., 2008). Due to the health benefits attributed to it, ginseng has been a major ingredient in traditional Chinese medicine for thousands of years, and continues to be used in herbal teas, energy drinks, and alcoholic beverages (Baeg & So, 2013). For example, Patel and Rauf (2017) reviewed the antioxidant, anti-inflammation, anti-fatigue, antitumour, antidiabetic, cardioprotective, antimicrobial and neuroprotective properties of ginseng. The medicinal properties of ginseng are associated with the presence of ginsenosides. Ginsenosides comprise a group of biologically active triterpene saponin compounds produced by Panax spp. through secondary metabolism (Lee & Kim, 2014). Each species has a different ginsenoside profile, and therefore is associated with different medicinal properties (Lu et al., 2008). It has been hypothesized that the primary role of ginsenosides in planta is one of plant defense due to their antimicrobial properties and bitter taste (Nicol et al., 2002; Oh et al., 2014).

Wild American ginseng (P. quinquefolius L.) is found sparsely distributed in well-shaded areas of moist, mature, hardwood forests (Vaughan et al., 2011). However, due to over-harvesting during the past centuries, ginseng is regarded as endangered in Canada (Vaughan et al., 2011). American ginseng is the primary species cultivated in North America (Baeg & So, 2013) and, in Ontario alone, ginseng production yielded more than $130 million in annual revenue in 2012, which has increased in in the following years, making it the province’s most valuable field-grown horticultural crop (Westerveld, 2014). The sandy soils, well drained moderate temperatures and moderate precipitation levels north of Lake Erie in southwestern Ontario, Canada are ideal for the commercial
cultivation of American Ginseng (Beyfuss, 2017). Once stratified, ginseng seeds are planted in the fall in raised-bed gardens, they germinate the following spring. Ginseng seed stratification is the process of maintaining a seed and moist sand mixture in a container over 21 months on average before ginseng garden seeding (Proctor & Stechyshyn-Nagasawa, 2008). This period of maintenance in specific temperatures encourages dehiscence and is required to break seed dormancy which is required before germination can occur (Lee et al., 2018). Once established, ginseng plants are then cultivated under the cover of shade cloths (to imitate forest canopy cover) for 3-5 years before harvesting at the end of summer (Beyfuss, 2017).

### 1.2 Ginseng Replant Disease

A major challenge for ginseng growers is the occurrence of ginseng replant disease (GRD). Ginseng replant disease is a persistent disease syndrome characterized by poor germination and plant establishment, and high levels of plant disease (especially root rot), leading to low plant density and therefore poor yields of ginseng root, when the crop is planted where ginseng has been cultivated previously (X. Li et al., 2011). Wild ginseng does not experience typical replant disease symptoms, likely due to the low density of established plants (Westerveld, 2014). Many monocultured and perennial crops, including apples (Mazzola, 1998), asparagus (Blok & Bollen, 1996), and stone fruits (Browne et al., 2013) experience replant symptoms with varying severity. In apple orchards, for example, replant symptoms such as root tip necrosis, reduced root biomass and stunted internodes displayed by affected trees can develop in as little as three months after planting in untreated, multigenerational apple orchards. However, soil fumigation and rootstock genotype selection consistently provide effective disease control (Mazzola & Manici, 2011). Fumigants, such as methyl bromide, have been heavily relied on for soil sterilization to prevent GRD symptoms, however methyl bromide was phased out after the 1987 Montreal Protocol on Ozone Depleting Substances due to its ozone depleting properties, leaving growers without an effective solution to GRD (United Nations Environment Programme, 2020). The persistence of GRD, and limited mitigation strategies, greatly limits the availability of suitable land for ginseng cultivation, as well as
the ability of growers to maintain gardens within a reasonable distance of their home farms. In point of fact, the Ontario Ginseng Growers Association (OGGA), a non-profit organization representing Ontario producers of ginseng, estimate that, without a viable solution to GRD, there will be no more suitable land for ginseng cultivation in Ontario within 20-30 years (Ontario Ginseng Growers Association, 2021). It is important to note that soils with high GRD potential do not inhibit the growth of other crops (T.S.C. Li, 1995).

Common symptoms of GRD include low seed germination percentage, severe root rot, reduced plant stand counts and reduced root size (Reeleder et al., 2002). Several factors have been implicated in the development of GRD including allelopathy/autotoxicity (X. Li et al., 2011), changes in soil chemical properties (Huang et al., 2013), and changing microbial compositions (Wu et al., 2015; Dong et al., 2016). During the ginseng cultivation period the garden soil becomes more acidic and toxic compounds, such as 1,4-diisopropylbenzene (DiPB), benzoic acid and hexadecanoic acid, accumulate in the soil, which also negatively affects the growth of ginseng plants (Dong et al., 2018). Similarly, apple replant soil has also been shown to contain an abundance of phenolic chemicals such as phlorizin, benzoic acid and vanillic aldehyde (Yin et al., 2016). A potential mitigation strategy to address the accumulation of allelochemical compounds in the soil is inoculation with arbuscular mycorrhizal fungus (AMF), such as *Acauloapora scrobiculata*. When peach seedlings grown in peach replant soil were inoculated with AMF there was significant decline in abundance of benzoic acid, benzaldehyde, diisooctyl phthalate, phenols, and sterols in the soil (Lu et al., 2019).

Ginsenosides accumulate in ginseng plants over the multi-year cultivation cycle. In *P. ginseng*, for example, the ratio of total ginsenosides/total dry root weight increases annually for three years, declines during the fourth year and increases again at the fifth and the sixth years (Samukawa et al., 1995). Ginsenosides are also found in the soil surrounding ginseng plants, through secretion and/or the breakdown of dead roots (Nicol et al., 2003) and decomposition of leaf litter.
Ginsenosides are mildly fungitoxic to some fungal species (e.g., *Alternaria panax, Trichoderma spp.*), but can also stimulate the growth of some ginseng pathogens (e.g., *Pythium irregulare, Illyonectria mors-panacis* (formerly *Cylindrocarpon destructans*)) (Nicol *et al.*, 2002; Nicol *et al.*, 2003, Ivanov & Bernards, 2012). It is possible that ginsenoside-enhanced pathogen growth contributes to the overabundance of pathogenic fungi and oomycetes in ginseng gardens, and the resulting increased competition for resources may contribute to the decrease in the relative abundance of bacterial and fungal species that benefit soil productivity, though this latter hypothesis has not yet been tested.

Ginsenosides have also been demonstrated to be autotoxic – i.e., toxic to the plant that produces them – particularly to seedlings grown in soils where adult plants have secreted high concentrations of ginsenosides (Yang *et al.*, 2015). For example, when freshly planted seeds were treated with ginsenoside solutions, seedling emergence, and subsequent plant biomass were significantly lower compared to controls, and none of the seedlings survived (Yang *et al.*, 2015). The presence of ginsenosides in soil, in combination with the other factors mentioned above, likely contributes to the development and persistence of GRD. Other perennial monoculture crops that experience replant disease, such as *Rehmannia glutinosa*, also demonstrated the accumulation of allelopathic autotoxic chemicals that include terpenoids and flavonoids (Li *et al.*, 2017).

Oomycota are a phylum of fungus-like microorganisms, informally known as oomycetes or water-moulds (Kamoun, 2003). Their functional and phenotypic similarity to fungi and relatively low abundance in soil has resulted in very little research focus on oomycetes as a taxon within microbiomes. The Oomycota includes several species known to be soil-borne plant pathogens that can infect ginseng, including *Pythium spp.* and *Phytophthora spp.* (Nicol *et al.*, 2003; Ivanov & Bernards, 2012; Meng *et al.*, 2014), and should therefore be considered in GRD research.
1.3 Studying the Microbiome

A microbiome is defined as the characteristic microbial community present within a specific habitat that has distinct physio-chemical properties. These properties are both dynamic and interactive over time and space (Berg et al., 2020). When studying the microbiome there are many parameters to consider, such as the diversity and richness of species present, the overall species composition, and the relative abundance of each species. Advances in high-throughput, next generation sequencing (NGS) and microbial sequence databases have allowed more extensive and comprehensive studies of microbial community structure and dynamics (Goodrich et al., 2014). Microbiome research now makes use of metabarcoding to identify the species present in the community of interest and estimate their relative abundance. This approach allows the extrapolation of many community parameters and comparisons between different samples (Caporaso et al., 2011).

Metabarcoding refers to the PCR amplification and sequencing of a target region of DNA that is conserved across a group of organisms (e.g., bacteria, fungi, or oomycota), but which also contains sufficient sequence variation that it can be used to identify subgroups, such as individual species, from within the target group (Taberlet et al., 2012). Briefly, the process of metabarcoding includes collection of a community sample (e.g., soil, water, etc.), DNA extraction, target gene amplification, high throughput, NGS of the amplified community DNA products, sequence processing and statistical analyses (Taberlet et al., 2012; Caporaso et al., 2012; Lynch & Neufeld, 2015). Metabarcoding can bypass some of the bias associated with underrepresentation of difficult to culture or non-culturable species as well as capturing species present in low abundance that would otherwise go undetected (Lynch & Neufeld, 2015). One of the greatest advantages of metabarcoding is the large volume of data that can be collected, processed, and analyzed in a reasonable amount of time (Taberlet et al., 2012, Caporaso et al., 2012). Another advantage is the reproducibility of results as demonstrated for the consistency in using the Illumina Miseq platforms (Caporaso et al., 2012). One important caveat regarding metabarcoding, however, is that community DNA samples can include extracellular DNA from dead cells or DNA from dormant microorganisms that are not a part of the
functioning microbiome (Lynch & Neufeld, 2015), and this can lead to an overestimate of the number of unique species active in the microbiome, or a misrepresentation of the functional microbiome. The chosen NGS platform will also have associated biases, most commonly introduced through library preparation, choice of primers and sequencing fidelity; however, most bioinformatic pipelines that process NGS data include quality filtering steps to minimize the downstream effects of said biases (Minoche et al., 2011; Schirmer et al., 2015).

1.4 Next Generation Sequencing Primers

The ideal primer set contains a pair of forward and reverse primers that bind to a specific region of a gene that is highly conserved within one specific group of organisms. To be useful for species identification, the primers also need to border a region with high enough variability to provide species-specific identification. Finally, the primers need to amplify an amplicon of an appropriate length that is compatible with the intended NGS platform (Alberdi et al., 2018).

The mitochondrial cytochrome c oxidase subunit 1 (COX1) is commonly used as a barcode for animal species, however the COX region in fungi can contain many introns depending on the fungal species, and the lack of sequence variation between species makes it a poor marker for fungal community studies (Dentinger et al., 2011; Schoch et al., 2012). Instead, the internal transcribed spacer (ITS) regions of the ribosomal gene cluster in fungi has been used as the “go-to” target for fungal metabarcoding as this region has been used successfully to amplify fungal DNA with high specificity (Schoch et al., 2012). The ITS region is comprised of 3 subregions: ITS1, 5.8S, and ITS2. Primers that target the ITS1 region have shown the greatest resolution (discrimination at the level of species), however, this region can range from 500 – 1000 bp (Scibetta et al., 2018). The advantages of the ITS2 region are lower length variation and more universal primer sites that result in less taxonomic bias (Nilsson et al., 2019). The length of the ITS2 region in most fungi fits the 2 × 300 bp length restriction of the Illumina Miseq platform, and has demonstrated reliable, high fold coverage of microbial communities.
(Taylor et al., 2016), and will therefore be used in this project for fungal amplification. Riit et al. (2016) modified ITS2 primers for oomycete metabarcoding and demonstrated increased specificity for oomycetes compared to previous primer sets, however these primers have not been used in a multiplexed, high throughput sequencing project such as the one described herein. These primers (Riit et al., 2016) will be used in an attempt to amplify oomycotan DNA from soil samples in this project.

1.5 Analysis of Next Generation Sequencing Data

Following DNA sequencing, sequences may be clustered based on shared sequence identity into OTUs, or operational taxonomic units (Taberlet et al., 2012) which are groups representing unique taxa. The percentage of shared identity is chosen by the researcher, with 97% commonly used as a cut-off for OTU clustering since 1994 when it was proposed for 16S rRNA sequencing as the threshold for identifying individuals (or reads) from a single species (Stackebrandt & Goebel, 1994; Edgar, 2018). While some argue the conventional usage of 97% is too low (or too high), this threshold allows reads from the same species to be clustered together even with errors introduced through PCR and sequencing (Huse et al., 2010).

A consensus sequence from each OTU is compared to sequence databases to identify the species present in each community sample. The relative number of times an individual OTU is found (the number of reads of this OTU compared to all retained reads in a sample) provides an approximation of the relative abundance of community members, and longitudinal studies can track changes in community parameters over time (Goodrich et al., 2014). Diversity is an important factor considered following sequencing of community data (Garbeva et al., 2004). Microbial diversity describes the complexity and variability of a microbiome, and it is influenced by the species richness, which refers to the number of unique species observed in a community, as well as the relative abundance and evenness of the different community members (Torsvik & Øvreås, 2002). Microbial diversity influences the stability and resilience of the microbiome and is often used to
compare the general health and productivity of the soil environment (Torsvik & Øvreås, 2002).

1.6 The Microbiome of Ginseng Garden Soil

The bacterial microbiome of ginseng gardens has been studied recently. For example, N.L. Nguyen et al. (2016) extracted community DNA from ginseng gardens after 0, 2, 4, and 6 years of cultivation. They collected what they termed healthy rhizosphere soil from the roots of plants that displayed dark green leaves, normal stems, and roots without lesions, and compared the microbial composition from this soil to “unhealthy” rhizosphere soil collected from roots of plants that demonstrated stem wilt, discoloured leaves and evidence of root rot. DNA was amplified using 16S bacterial DNA primers and OTUs were clustered at 97% sequence similarity. Overall, there was a significant decrease in bacterial Shannon diversity values over cultivation time. It was proposed that factors such as nutrient depletion, phosphorous deficiency, and lower pH in older ginseng gardens resulted in the reduced bacterial diversity. Although I will not be studying the bacterial microbiome, the previously mentioned factors affecting the bacterial community structure likely affect the fungal and oomycotan communities as well.

Dong et al. (2017) similarly used high-throughput sequencing to characterize changes in the soil microbiome of ginseng gardens. They used 18S DNA primers to classify a relatively small number of reads, 38,372 bacterial sequences and 29,415 fungal sequences, from 21 soil samples after clustering their sequences at 97% shared sequence similarity. Over three years of cultivation, fungal Shannon diversity indices and Chao1 richness indices significantly decreased and the ratio of fungi to bacteria increased. The relative abundance of Pleosporales, Lecanorales, Calosphaeriales, Capnodiales and Eurotiales increased throughout the three-year cultivation time and the relative abundance of Corticiaceae, Agaricales, Verrucariales and Tremellales decreased. I predict my data will demonstrate similar trends in regard to fungal diversity and the relative abundance of these species over time. However, by sampling multiple times per year, I aim to identify when these characteristic changes occur with more precision.
Dong et al. (2017) used metabarcoding to compare the fungal and bacterial soil microbiome present in ginseng gardens and maize fields over three years of cultivation. Both community composition and relative abundance of bacterial and fungal species were significantly different between ginseng garden soil and maize soil. Consistent with their 2016 findings, the ratio of fungi to bacteria increased in ginseng garden soil compared to maize soil, which can imply a change in soil productivity (Dong et al., 2016). Soil productivity is measured as the rate of increase in the weight of organic matter present in the soil over a period of time (Westlake, 1963). Soil organic matter holds important nutrients plants require for growth and reproduction, and it also improves the ability of the soil to retain water (Lal, 2009). Dong et al.’s (2017) results also demonstrated a decline in bacterial diversity and an increase in fungal diversity in ginseng soils throughout cultivation time. The increase in fungal diversity contradicted their previous results (Dong et al., 2016), which demonstrated a decrease in fungal diversity. However, the more recent finding (Dong et al., 2017), that fungal diversity increases in the ginseng garden soil microbiome, is consistent with other monoculture crops that experience replant syndromes such as peanuts (Chen et al., 2016) and peaches (Benizri et al., 2005). Since measures of diversity combine the number of unique species present as well as the relative abundance of each species, the inconsistencies between the two papers by Dong et al. could arise from a decrease in the number of different species but a large increase in the abundance of pathogenic species. My project will also compare the changes in overall fungal diversity and the relative abundance of taxa present in ginseng garden soils, however the samples will be compared to soil in the same garden that is not being used to grow ginseng. While I am not investigating the bacterial microbiome, I expect to find a similar increase in fungal diversity throughout cultivation time.

Liu et al., (2019) used metagenomic sequencing to study the relationship between specific microbial taxa and GRD. Metagenomic sequencing is similar to metabarcoding, though it is used to study all the DNA in an environment and does not target specific marker genes such as 16S or ITS (Daniel, 2005). After sequence annotation it was demonstrated that Ilyonectria was enriched in GRD diseased roots, and Mortierella was increased in healthy roots and the relative abundance of Actinomycetales decreased in
diseased roots while *Pseudomonadales* increased. *Ilyonectria mors-panacis* is a fungus known to cause root-rot disease and rusty root symptoms in ginseng (Farh et al., 2018). Identifying changes in the relative abundance of genera or species with known pathogenic abilities could be informative as to their role in causing or supporting GRD. In my research I will track changes in the relative abundance of known pathogens previously isolated from diseased ginseng such as *Pythium* spp., *Phytophthora* spp. (Reedeler & Brammall, 1994) and *Ilyonectria* spp. (Farh et al., 2018).

Soil microbial diversity is critical to soil health, quality, and functionality. Soil microbes have a variety of roles in the soil environment including decomposition of organic matter, nutrient cycling, and toxin removal (Garbeva et al., 2004). They also interact with other biotic factors such as plants, nematodes, and other microbes, and are proposed to greatly influence the susceptibility of plants to disease (Abawi & Widmer, 2000). Plant type, soil properties (e.g., pH, nutrient levels, % composition, texture etc.) and agricultural management routines are the largest influences on microbial community structure (Garbeva et al., 2004). Some researchers describe soils as disease-suppressive as they reduce the ability of pathogens to survive, therefore reducing the harm to surrounding plant life. In general, the higher richness and diversity present in the soil, the less severe pathogen attacks will be (Hyakumachi, 1996). While the mechanisms of soil disease suppression are not well understood, it has been deduced that the cause is microbial because soil sterilization removed the suppressive abilities of the soil (Malajczuk, 1983). As discussed above, significant changes in the diversity of the soil microbiome in ginseng garden are occurring throughout ginseng cultivation.

Dong et al. (2018) demonstrated that inoculating GRD soil with bacteria that have toxin degrading abilities, therefore also increasing the bacterial richness, reduced the concentration of toxic compounds in the soil and improved overall ginseng growth. Y. Li et al. (2019) demonstrated that pairing reductive soil disinfestation, to remove soil pathogens, and the application of a maize cover crop, to restore microbial diversity, effectively reduced the effects of GRD. However, they proposed additional measures, such as microorganism inoculation, be used in parallel to further reduce the severity of GRD and promote the growth of healthy ginseng with high yields in commercial gardens.
The soil microbiome is an important factor in understanding the development and persistence of GRD, and while general trends have been described, more specific characterization of the shifts in the microbial community composition are required to address the effective management of GRD.

The factors driving changes in the soil microbiome are also important to consider. There is evidence that the presence of ginsenosides in *P. notoginseng* garden soil can influence the fungal and bacterial microbiome through the utilization of ginsenosides as a carbon source during the first 30 days following inoculation. Species that could utilize ginsenosides as a carbon source were enhanced and species without the ability to modify ginsenosides were suppressed (Luo et al., 2020).

### 1.7 Research Objectives

The first objective of my research project is to develop Illumina Miseq-compatible primers for oomycetes and apply them to a NGS microbiome study. The second objective is to track changes in the fungal community composition in newly planted ginseng garden soil throughout the first two years of cultivation. I hypothesize that throughout ginseng cultivation the composition of the soil microbiome will shift towards a profile characteristic of ginseng replant disease. Identifying key changes in the soil microbiome of ginseng gardens throughout cultivation can confirm previous characterizations of GRD related microbial community changes and introduce new information about oomycete communities into GRD microbiome research. Gathering more information regarding the characterization of ginseng garden soil and the changes that occur throughout cultivation will provide a more comprehensive understanding of the ginseng garden microbiome and GRD.
2. Methods

2.1 Sampling Locations

Three newly-planted ginseng gardens in Southwestern Ontario were identified and made available for soil sampling in collaboration with OMAFRA (http://www.omafra.gov.on.ca/english/) and the Ontario Ginseng Growers Association (OGGA; https://ginsengontario.com/). The gardens are located within Norfolk County (Figure 1) where the annual average precipitation is 945 mm/year (Appendix C) and the soil is described as sandy loam (Table 1). Norfolk County is rated as 6b on the Canadian Plant Hardiness Zone scale (http://www.agr.gc.ca/atlas/agpv?webmapen=78529700717d4cab81c13e9f9404ef10&webmap-fr=c1b454842d3748b0bb0807d7817d34e2) . While the complete histories of the ginseng gardens used in this study are not known, none have been used previously for ginseng cultivation. Common crops grown in Norfolk County include maize, tobacco and different grains. Samples were collected in the fall of the planting year (2018) and four times a year (spring, early summer, late summer and fall) for two consecutive years (2019 & 2020).

**Figure 1: Location of Study Garden Sites.** Modified Google Maps ™ image obtained May 2019, showing the approximate locations of the three garden study sites in Norfolk County, Southwestern Ontario, Canada. Precise location information is withheld to protect grower privacy.
2.2 Field Sampling

Soil samples were collected using a LaMotte 1055 soil sampler (2.5 cm diameter, 30.5 cm long) that was sterilized with ethanol and rinsed with distilled water between sampling sites. Samples were collected on dry days to prevent the spread of water borne pathogens and so the soil environment was representative of the average moisture level, not post rainfall. Three soil cores were taken from each of five locations within a chosen bed in each garden and pooled for each location (N=15) to create a representative soil sample. Each sampling location within a garden site was approximately 3.6 m apart, in a line along the center of the garden bed (Figure 2). Garden samples were taken from the center of a middle bed, a minimum of 5 bays in from the perimeter of the garden. This location was marked with orange tape on an adjacent post to ensure samples were taken from the same bed on every sampling date. Trench samples were taken from between adjacent beds in which ginseng was planted; these sites had no ginseng plants, but experienced the same grower treatments (e.g. fungicides, insecticides) and environmental conditions (e.g. shade cloths). Control samples were taken from outside the garden perimeter where the soil is the same as the garden soil composition but was not subject to the same agronomic inputs as Garden beds or the influence of ginseng plants. Three pooled cores yielded approximately 500 g of soil, which was placed in freezer bags in a cooler for transport then stored -20 °C until analyzed.
Figure 2: Representation of a ginseng garden showing sampling locations. Red boxes indicate garden sampling locations, blue boxes indicate trench sampling locations and green boxes indicate control sampling locations.

Approximately 260 g of soil from each garden was sent to A&L Biologicals (https://www.alcanada.com/) in London, ON for analysis of nutrient availability, minerals, soil pH, %clay/silt/sand composition, and water holding capacity (Appendix B).

Table 1: Ginseng Garden Soil Properties. Percent composition of soil measured by the Hydrometer method by A&L Canada Laboratories Inc.

<table>
<thead>
<tr>
<th></th>
<th>Sand (%)</th>
<th>Silt (%)</th>
<th>Clay (%)</th>
<th>Soil Texture Class</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site 1</td>
<td>82.9</td>
<td>10.5</td>
<td>6.6</td>
<td>Loamy Sand</td>
</tr>
<tr>
<td>Site 2</td>
<td>76.9</td>
<td>14.5</td>
<td>8.6</td>
<td>Sandy Loam</td>
</tr>
<tr>
<td>Site 3</td>
<td>84.9</td>
<td>6.5</td>
<td>8.6</td>
<td>Loamy Sand</td>
</tr>
</tbody>
</table>

2.3 Molecular Protocols

Approximately 5 g of soil from each of the three soil cores per sample were combined in a bag creating a sample composite and mix thoroughly. DNA was then extracted from 0.1 g of the soil from each sample composite using the ZymoBIOMICS DNA Microprep
kit™ (Zymo Research ©, Irvine and Tustin, California), according to manufacturer’s instructions, using a Vortex Genie® bead beater system (Scientific Industries, Inc., Bohemia, New York). Extracts were stored at -20 °C in 1.5 mL microcentrifuge tubes. DNA was also extracted from fungal (Fusarium oxysporum and F. graminearum) and oomycete (Phytophthora parasitica, P. sojae and Pythium irregulare) cultures to be used as positive controls during PCR amplification. Extracted DNA samples were PCR-amplified using two sets of DNA primers targeting the ITS2 region of the small-subunit ribosomal RNA of fungi (Taylor et al., 2016) and oomycetes (Riit et al., 2016) (Table 2). Both primer sets create amplicons of approximately 500 bp. The primer sequences also contained short adapter sequences (15 bp) on the 5' end that facilitate barcoding and Illumina adapter sequence incorporation in the second round of PCR (Figure 3).

**Table 2: First round PCR primers.** The short adapter sequence necessary for the second round PCR primers to bind to the template, is shown in red, next to the 15 bp linker sequence (black text) preceding the primer sequence that hybridizes to the conserved regions flanking the gene region to be amplified in fungi (blue text) and oomycetes (green text).

<table>
<thead>
<tr>
<th>Reference</th>
<th>Name</th>
<th>Direction</th>
<th>Sequence (5' -&gt; 3')</th>
</tr>
</thead>
<tbody>
<tr>
<td>Taylor et al., 2016</td>
<td>5.8S-F</td>
<td>Forward</td>
<td>TCGTCGGCAGCGTCAGATGTGTATAAGAGACAAGAACCTTTYRRCAAYGGATCWCT</td>
</tr>
<tr>
<td>Taylor et al., 2016</td>
<td>ITS4-R</td>
<td>Reverse</td>
<td>GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAAGACCTTCCGCTTATTGATATGCTTAART</td>
</tr>
<tr>
<td>Riit et al., 2016</td>
<td>ITS3oo-F</td>
<td>Forward</td>
<td>TCGTCGGCAGCGTCAGATGTGTATAAGAGACAGAGTA&lt;sup&gt;TGYYGTATCGT&lt;/sup&gt;</td>
</tr>
<tr>
<td>Riit et al., 2016</td>
<td>ITS4-R</td>
<td>Reverse</td>
<td>GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAGAGTA&lt;sup&gt;TGYYGTATCGT&lt;/sup&gt;</td>
</tr>
</tbody>
</table>
PCR was carried out using Acustart II PCR Toughmix Taq polymerase (Quantbio). Each sample was amplified twice, using two different volumes of DNA (1 and 4 μL) to account for the variation in DNA concentrations between samples. Samples were separated on a 1% agarose gel, tracked during electrophoresis with TrackIt™ Cyan/Yellow (6X) Loading Buffer (ThermoFisher Scientific) and stained using SafeView Classic™ DNA Dye (abm©). Product size was confirmed by comparison to bands in the Invitrogen™ 1 kb Plus DNA Ladder (ThermoFisher Scientific).

The resulting PCR products from both the 1 μL and 4 μL of template DNA were pooled before a second round of PCR-amplification for samples that provided a detectable amount of amplification on a 1% agarose gel, otherwise only the 4 μL sample was used as some 1 μL reactions did not produce visible bands. The second round of PCR used forward and reverse DNA primers that contained sequences complementary to the small adapter sequences incorporated during the first round PCR step (Herbold et al., 2015) linked to one of a series of 8 bp ("barcodes") and a large adapter sequence (F=29 bp, R=24 bp) for NGS compatibility to yield the second round PCR products (Figure 3). Barcodes were selected from the Illumina Adapter Sequences document found on the Illumina Support website (https://support.illumina.com.html).
Figure 3: Two-step PCR approach to amplify and prepare sample DNA for 2x300 Illumina Miseq NGS. The first round PCR uses primer sequences (red) specific to the gene of interest (navy) to create DNA products (light blue) with small adapter sequences (green) on both the 3' and 5' ends. The second PCR step uses primers that bind to the small adapter sequences (green) on the ends of the PCR product, then amplifies a product that has the template DNA (first round PCR product) and a large adapter sequences (purple) on both the 5' and 3' end, separated by a unique barcode (yellow) for each sample. Second round PCR products are then able to bind to the Illumina flow cell for DNA sequencing. The DNA template sequence and the barcode sequence are read separately, and electronically paired. Therefore, Illumina sequence reads can be sorted into their original samples by their paired index reads.
2.4 PCR Conditions

First round PCR was carried out using 1.25 μL of both the forward and reverse primers (5 μM), 12.5 μL 2× ToughMix (Quanta Biosciences), 0.5 μL of 50× dye and either 1 or 4 μL of template DNA, with molecular grade water bringing the total volume to 25 μL. PCR amplification was carried out in a Biometra T1 Thermocycler using the following programming; 95 °C for 2 minutes, 30 cycles of 95 °C for 30 seconds, 55 °C for 30 seconds, 72 °C for 30 seconds, and after cycling, holding at 4 °C. PCR products were confirmed using gel electrophoresis using 1 % (w/v) agarose gels in 1× TAE buffer and a BIO-RAD PowerPac 3000 supplied electrical current. For the second round PCR 1.0 μL of QIAquick purified first round PCR product was used along with 0.8 μL of both forward and reverse primers, 10 μL of 2× Toughmix, 0.5 μL of 50× dye and molecular grade water bringing the total volume to 20 μL. PCR amplification was carried out using the following program: 95 °C for 5 minutes, 95 °C for 30 seconds, 55 °C for 30 seconds, 72 °C for 1 minute, and hold at 10 °C.

Product size was confirmed on a 1% agarose gel (as above) and submitted to the London Regional Genomics Centre (LGRC) in the Robarts Research Institute (http://www.robarts.ca/london-regional-genomics-centre) in London, ON for size selection using a 1.5% Agarose Pippin Prep Gel Cartridge (D-Mark Biosciences) and sequencing by paired-end 2 × 300 Illumina Miseq High Throughput Sequencing. Size selection was necessary to remove off-target sequences smaller than 250 bp and larger than 1.5 kb that remained after PCR amplification.
2.5 Illumina Miseq NGS Sequencing

The 29 bp (Forward primer) or 24 bp (Reverse primer) adapter sequence on the 5’ end of the second round PCR products binds to the Illumina flow cell to facilitate sequencing. Sample barcodes allow the pooling of multiple samples before being sequenced in one multiplexed 2 × 300 Illumina Miseq next generation sequencing (NGS) run. The resulting sample reads can then be sorted into their original samples by the corresponding barcode sequence. Two soil sampling dates (150 samples) were pooled into one Illumina run, and 4 Illumina runs were performed.

2.6 Bioinformatic Analysis

Raw FASTQ sequencing data was initially processed using the QIIME 2 pipeline for Illumina Miseq demultiplexed single-end data (Boylen et al., 2019). Quality plots were used to determine the parameters for denoising the reads using the DADA2 plugin (Callahan et al., 2016). The DADA2 plugin removes low quality and chimeric sequences, and sequences blow 0.001% total abundance were removed. An alpha rarefaction plot was created to ensure all the richness in the samples was observed and a maximum sampling depth of 15000 was chosen because it approximately the median frequency per sample (Appendix D). Individual reads were clustered into operational taxonomic units (OTUs) based on 97% shared sequence identity before performing open-reference clustering based on 97% shared sequence identity. Taxonomy was then assigned using a trained classifier based on the UNITE ITS sequence database (Nilsson et al., 2019). Some unidentified sequences were manually updated after individual BLASTn searches. Uchime was used to identify chimeric sequences not removed by DADA2, and OTUs with a total relative abundance less than 0.001% were removed.
2.7 Statistical Analysis

Species Chao1 richness, Shannon diversity, Pielou evenness, and Bray-Curtis dissimilarity were determined by analyzing the high-throughput sequence data using R statistical packages. Chao1 richness is an estimate of the number of species present in a community and it is computed using species abundance data with emphasis of the abundance of rare taxa (Chao & Bunge, 2002). Shannon diversity combines measures of species richness and abundance, and its assigned indices represents the uncertainty about the identity of an unknown individual (Morris et al., 2014). Evenness represents how the microbial species, and their abundance is spread over a specified habitat, and dominance is the degree to which one species is more abundant than the rest (Morris et al., 2014). Finally, Bray-Curtis Dissimilarity is used to quantify how dissimilar the microbial composition is between two different sampling sites by comparing the number of shared species (Faith et al., 1987). Packages Microbiome (Lahti et al., 2017), vegan (Oksanen et al., 2019), and ade4 (Dray & Dufour, 2007) were used to calculate several diversity measures and perform statistical analyses such as adonis (PERMANOVA) and anova tests to identify significant differences between different groupings of data. The phyloseq package (McMurdie & Holmes, 2013) was used to restructure data and create ordination plots, and ggplot2 (Wickham et al., 2011) was used to create heatmaps of species relative abundance for each sampling location and treatment. ANOSIM tests, included in the vegan package, were used to determine if there were significant differences between Garden and Control samples within each Site. ANOSIM was chosen because it is a non-parametric test that uses a ranked dissimilarity matrix and does not require equal dispersion and makes the fewest assumptions about the data.
2.8 Fungal and Oomycete Cultures

Fungal and oomycete cultures were obtained from various sources and maintained to provide PCR positive control DNA templates (Table 3).

**Table 3: Cultured fungi and oomycetes.** Fungal and oomycete cultures maintained from fall 2018 to fall 2020 on V8 juice agar.

<table>
<thead>
<tr>
<th>Organism Type</th>
<th>Species</th>
<th>Strain</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fungus</td>
<td><em>Fusarium oxysporum</em></td>
<td>481/428</td>
<td>Western University Fungal Collection</td>
</tr>
<tr>
<td>Fungus</td>
<td><em>Fusarium graminearum</em></td>
<td>524/525</td>
<td>Western University Fungal Collection</td>
</tr>
<tr>
<td>Oomycete</td>
<td><em>Pythium irregulare</em></td>
<td>598</td>
<td>Canadian Collection of Fungal Cultures</td>
</tr>
<tr>
<td>Oomycete</td>
<td><em>Phytophthora parasitica</em></td>
<td>310</td>
<td>Dr. Franck Panabières, INRA, France</td>
</tr>
<tr>
<td>Oomycete</td>
<td><em>Phytophthora sojae</em></td>
<td>2a</td>
<td>Dr. Mark Gijzen, Agriculture Canada</td>
</tr>
</tbody>
</table>

All species were cultured in standard 9 cm petri dishes on V8 media (15 g agar, 3 g calcium carbonate, 800 mL distilled water, 200 mL V8 juice (Campbell’s Soup Co.), 1.5 % (w/v) agar. Cultures were kept in the dark at room temperature and were re-plated approximately every 6 weeks.
3. Results and Discussion

This project had two main objectives: 1) to obtain Illumina MiSeq-compatible primers for oomycetes and apply them to a NGS study, and 2) to track changes in the soil fungal and oomycotan community profiles in ginseng garden soil, starting with newly planted ginseng gardens (with no history of prior ginseng cultivation), throughout the first two seasons of ginseng cultivation. Soil sampling several times throughout each season of cultivation provided a time-series of soil DNA to establish fungal and oomycotan community profiles that will allow me to characterize changes that occurred in the mycobiome of these sites during continuous cropping of ginseng.

3.1 Obtaining Illumina Miseq Compatible Primers for Oomycetes

An objective of this project was to obtain oomycete-specific DNA primers that were compatible with Illumina Miseq NGS in order to characterize the oomycete microbiome of ginseng gardens. Several oomycete species have been identified as efficient ginseng pathogens (Y. Li et al., 2020; Luo et al., 2020), yet they are often missing from metabarcoding NGS ginseng studies. Oomycetes are morphologically similar to fungi, however since they are more closely related to algae, many species are not detected by available fungal primers. This prevents accurate oomycete community composition characterization. Oomycetes are also distinct from fungi in that they are either diploid or polyploid in their vegetative state, they contain cellulose in their cell walls and employ many different biochemical pathways such as the lysine synthesis pathway (Thines, 2018).

Gene targets that are conserved in oomycete species have been identified that may provide an option for NGS primer development. These include the histone 3 gene (HIS3) and translation elongation factor 1 (TEF1) (Carbone & Kohn, 1999; Crous et al., 2004; Lombard et al., 2015; Farh et al., 2019). These genes were considered in this study as they contained enough sequence variation to allow the differentiation of closely related species of important pathogen genera such as Phytophthora, Pythium and Alternaria, but
there are currently no published NGS-compatible, DNA primers targeting these genes. I chose multiple sets of HIS3 and TEF1 DNA sequences that were conserved across the majority of oomycete species and flanked a ~300 bp region of sequence with significant variation among different species. After applying multiple developed sets of DNA primers to *Pythium irregulare*, *Phytophthora sojae* and *P. parasitica* DNA extracted from cultures, and attempting to amplify the DNA with a range of annealing temperatures, only a small, inconsistent amount of amplification was achieved. PCR products were sent to the London Regional Genomics Center for Sanger sequencing, but the returned sequences did not correspond with the expected HIS3 or TEF1 gene sequences. Therefore, none of the developed primers were used to characterize the oomycotan microbiome in this study, but the HIS3 and TEF1 gene regions may be possible targets for future developmental work.

Next, I began optimizing conditions for published DNA primers (forward primer ITS3oo and universal reverse primer ITS4) for oomycete amplification and species barcoding (Riit *et al.*, 2016). The Riit *et al.* primer set targets the ribosomal ITS2 gene region, typically used for fungal barcoding, with increased specificity for oomycete DNA compared to other available primers. The primers were used successfully to amplify oomycete DNA extracted from cultured *P. parasitica* and *Pythium irregulare*, and did not amplify fungal DNA extracted from a culture of *Fusarium oxysporum*, demonstrating their selectivity for oomycete DNA (Figure 4). However, there was no amplification when DNA extracted from my soil samples was used as a PCR template. From this I concluded there was an insufficient amount of oomycete DNA in my soil samples for successful amplification and subsequent NGS. However, to be more certain of this conclusion we obtained soils with known oomycete-disease and, using the same soil extraction and PCR protocols, were successful in amplifying oomycete DNA (Figure 4). Thus, while the oomycete-specific primers described herein appear suitable for the amplification of oomycete DNA for NGS, fulfilling my first objective, their future

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1 Note that this control experiment was conducted by Andrew Rabas, a contemporary lab member working on a separate GRD project.
application in microbiome research will depend on higher concentrations of oomycete DNA in environmental samples. As a result, these oomycete primers were not used in addressing my second objective and oomycetes were not tracked in ginseng garden microbiomes in this study. Future application of oomycete-specific primers will require optimization of DNA extraction from sandy soils, such that species present in low abundance are better represented and an accurate characterization of the oomycete soil community can be achieved. This can also aid in removing bias in microbial diversity and species richness estimates, as well as overestimates of fungal diversity that result from oomycetes being incorrectly amalgamated with fungi. Furthermore, since oomycetes have an ITS2 region that varies in sequence length, often approaching the upper limit of Illumina Miseq NGS, amplifying the ITS2 DNA from all oomycete species may not be compatible with NGS metabarcoding.
Figure 4: DNA amplification using oomycete specific DNA primers.
Gel electrophoresis image of PCR products produced by oomycete-specific DNA primers targeting the ITS2 gene region. Riit et al. (2016) primers were used to amplify DNA extracted from cultures of *Pythium irregulare* (1), *Fusarium oxysporum* (2), and *Phytophthora parasitica* (3), as well as DNA extracted from bulk soil (4) and rhizosphere soil (5) collected from an oomycete-diseased ginseng garden. Resulting amplicons were between 500-600 bp. Amplicons for lanes 4 and 5 were generated by Andrew Rabas as part of ongoing optimization of oomycete NGS barcoding in the lab.
3.2 Analysis of the ginseng garden mycobiome

The initial sample set contained 390 soil samples taken from 3 ginseng garden sites, and 3 “treatments” within each garden site, from 9 sampling dates (note that the first sampling date only had 2 treatments). Five replicate samples were taken from each treatment at each date (Table 4). PCR amplicons from these samples were split into four Illumina Miseq runs which produced a total of 23,029,197 reads with an average of 65,154 reads per sample (Table 5). Removal of low-quality reads, however, yielded an incomplete dataset, as many samples produced no useable reads. With no option for resequencing, the available samples were re-assessed and pooled or discarded to yield a useable set of data. Specifically, several Trench and Summer B samples had only 0-2 useable replicates, so Trench samples and Summer B samples (samples collected in late August) were removed. This resulted in 206 samples remaining (Table 4), represented by 13,421,824 reads. After filtering out low quality reads, 6,480,343 reads remained, with an average of 31,611 reads per sample (Table 5B).

Four Summer A samples collected in 2020, two from Site 2 Garden and two from Site 3 Garden, also did not yield useable reads, but as these samples still had 3 reliable replicates out of 5, the three replicates were averaged to represent Summer 2020 Garden samples from Sites 2 and 3 in the resulting OTU table.
Table 4: Soil samples from three ginseng farms collected over a two-year period, from Fall 2018 to Fall 2020. Genomic DNAs were extracted, the ITS2 region amplified, sequenced in four Illumina 2×300 MiSeq runs, and the reads demultiplexed and processed from a total of 390 samples. Values indicate the number of soil samples taken, each representing 3 pooled soil cores, with the number of retained replicates of quality sequence data in parentheses. Numbers in bold indicate samples retained for downstream statistical analyses. No Trench samples were taken in Fall 2018. As a result of inconsistent recovery of sequence data from Summer B (2019 and 2020) and Trench samples, these were removed from downstream statistical analyses. G = garden samples, T = trench, and C = control samples.

<table>
<thead>
<tr>
<th>Sampling Date</th>
<th>Site 1</th>
<th>Site 2</th>
<th>Site 3</th>
<th>Sum</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>G</td>
<td>T</td>
<td>C</td>
<td>G</td>
</tr>
<tr>
<td>Fall 2018</td>
<td>5</td>
<td>0</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Spring 2019</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Summer A 2019</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Summer B 2019</td>
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<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Fall 2019</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Spring 2020</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Summer A 2020</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Summer B 2020</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Fall 2020</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>45</td>
<td>40 (36)</td>
<td>45 (40)</td>
<td>45 (38)</td>
</tr>
<tr>
<td><strong>Total Retained</strong></td>
<td>35</td>
<td>0 (0)</td>
<td>35 (35)</td>
<td>33 (33)</td>
</tr>
</tbody>
</table>
After filtering out low quality reads, Summer B samples and Trench samples 6,480,343 reads resulted with an average of 31,611 reads per sample. Further analyses were completed using data from 206 samples, collected from 3 gardens, 2 Treatments from within each Garden and from 7 sampling dates (Table 4).

Table 5: Summary of Illumina Miseq reads processing using quality control plugin DADA2. Includes the sum and average number of reads from all soil samples taken from ginseng garden and control soils (A) and retained samples after removing between-bed samples and Summer B samples (B). The initial number of reads returned after NGS was 23,029,197, but the number of reads used in subsequent analyses was 6,480,343.

<table>
<thead>
<tr>
<th></th>
<th>Input Sequences</th>
<th>Filtered Sequences</th>
<th>Denoised Sequences</th>
<th>Non-Chimeric Sequences</th>
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<tbody>
<tr>
<td><strong>A</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sum</td>
<td>23,029,197</td>
<td>12,254,017</td>
<td>11,578,375</td>
<td>9,263,491</td>
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<tr>
<td>Average/Sample</td>
<td>61,411</td>
<td>32,677</td>
<td>30,876</td>
<td>24,703</td>
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<table>
<thead>
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<th></th>
<th>Input Sequences</th>
<th>Filtered Sequences</th>
<th>Denoised Sequences</th>
<th>Non-Chimeric Sequences</th>
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<tbody>
<tr>
<td><strong>B</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sum</td>
<td>13,421,824</td>
<td>7,264,675</td>
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<tr>
<td>Average/Sample</td>
<td>65,472</td>
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<td>34,606</td>
<td>31,611</td>
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</tbody>
</table>

Reads were clustered at 97% sequence identity into 2,247 OTUs. Uchime was used once again to check for chimeric sequences and an additional 26 OTUs were removed. Though the vast majority of reads and OTUs belonged to the Kingdom Fungi as expected, the few non-fungal OTUs were removed as well as OTUs with less than 0.001% relative abundance, resulting in 1673 retained OTUs represented by 5,475,931 reads (Table 6). From the retained OTUs, a total of 475 unique genera and 672 unique species were identified, belonging to 12 fungal phyla (Table 6). Approximately 86.8% of retained reads, and 67.5% of OTUs, represented members of the fungal phylum Ascomycota. The
phylum Basidiomycota was the next most abundant, with approximately 18.6% of retained reads, and 6.9% of OTUs. While using ITS primers for NGS is associated with an inherent bias due to the shorter nature of the ITS region in Ascomycota, which is therefore easier to amplify (Banchi et al., 2018), this result is expected as many soil fungi belong to the phylum Ascomycota (Egidi et al., 2019). Broadly, 850 OTUs were found in all three sites, less than 160 OTUs were shared between 2 out of the 3 sites, and between 96-210 OTUs were found in just one site (Figure 5).
Table 6: Kingdom and phylum level classification of 1673 OTUs identified from 5,475,931 retained sequence reads. Summary of retained reads after removing low abundance OTUs, low quality OTUs, rarities (<0.001% relative abundance) and non-fungi OTUs, recovered from 206 samples of ginseng garden and adjacent control soils, collected from fall 2018 to fall 2020, inclusive.

<table>
<thead>
<tr>
<th>Phylum</th>
<th>Retained OTUs</th>
<th>% of Retained OTUs</th>
<th>% Of Total Relative Reads</th>
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</thead>
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<tr>
<td>Aphelidiomycota</td>
<td>3</td>
<td>0.18</td>
<td>0.12</td>
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<tr>
<td>Ascomycota</td>
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<td>67.54</td>
<td>86.79</td>
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<td>Basidiomycota</td>
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<td>0.01</td>
</tr>
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<td>0.01</td>
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<td>0.09</td>
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<tr>
<td>Kickxellomycota</td>
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<td>0.12</td>
<td>0.01</td>
</tr>
<tr>
<td>Mortierellomycota</td>
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<td>1.97</td>
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<td>Mucoromycota</td>
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<td>1.37</td>
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<td>0.41</td>
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<tr>
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<td>2.99</td>
<td>2.49</td>
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<td><strong>SUM</strong></td>
<td><strong>1673</strong></td>
<td><strong>100</strong></td>
<td><strong>100</strong></td>
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Since I collected samples from three independent ginseng gardens and associated control areas it was important to establish whether the fungal profiles from each were sufficiently similar to be able to pool the data. Bray-Curtis dissimilarity indices were calculated for each replicate from each site (N=3) and were pooled by Treatment and Date. The resulting values were analyzed using a repeated measures PERMANOVA, revealing significant differences in the species composition of the soil mycobiome between each site in both Garden ($F_6=1.89$, $p=0.01$) and Control ($F_6=1.50$, $p=0.02$) samples (Figure 6). Therefore, all further analyses were repeated independently on data from each individual site.
Figure 6: PCoA ordination plots of Control and Garden mycobiome composition. Bray-Curtis Dissimilarity indices are plotted for Control (top) and Garden (bottom) mycobiome data established for all three garden sites, including data collected from fall 2018 to fall 2020 inclusive. Sampling location is indicated by different colours, red = Site 1, green = Site 2, blue = Site 3.
An ANOSIM analysis of the Bray-Curtis indices established that the species composition of the soil microbiome differed significantly throughout the first two years of ginseng cultivation within both Garden and Control samples across all three sites (Table 7; Figure 7). The ANOSIM analysis supported the hypothesis that the microbial community structure changes over time, in Garden and Control samples at each Site. A relatively high R statistic indicates between group (data collected on different sampling dates) variation is higher than within group (data from one sampling date) variation, and the P value indicates how significant the differences in composition are between group communities (Anderson & Walsh, 2013). However, these changes needed to be further characterized over the next several years until these garden sites are harvested to establish how the mycobiomes changed and whether the same changes were occurring in both Garden and Control sites, or if they equally changed in different ways. Ultimately, the main drivers initiating the shifts in soil environment will need to be established before changes in the microbial community structure can be linked to the development of GRD, but this analysis determined soil microbial species composition is changing during cultivation.

Species diversity is a complex measure that considers the number of species, also known as species richness, and relative abundance, also known as species evenness. These parameters allow us to compare how diverse an ecosystem is compared to others. In my study, fungal community diversity (Shannon) and richness (Chao1) were tracked over time (Figure 8). An ANOVA test was first used to determine whether Date and/or Treatment, as well as a Date:Treatment interaction, significantly influenced diversity and richness values across sampling times. Shannon Diversity differed significantly between different sampling dates in sites 1, 2 and 3 (F₆=5.88, p=8.29e-05; F₆=4.45, p=9.94e-04; F₆=4.80, p=5.45e-04, respectively). Similarly, Chao1 Richness also differed significantly across time in sites 1, 2 and 3 (F₆=7.56, p=5.83e-06; F₆=11.95, p=1.73e-08; F₆=10.41, p=1.21e-07, respectively). Shannon Diversity and Chao1 Richness were not significantly influenced by Treatment or a Date:Treatment interaction when 0.05 was the chosen significance level.
Table 7: Changes in microbial composition over time. An ANOSIM test of the ranked dissimilarity matrix (Bray-Curtis Dissimilarity indices) was used to determine whether significant differences existed in the microbial composition of Garden and Control samples across time. Significant differences in microbial composition across time, but within a specific set of Garden or Control samples within a single site are indicated with an * = (p<0.001).

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<th>Control</th>
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<td>$P$ value</td>
<td>R Statistic</td>
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<td>1e-04*</td>
<td>0.41</td>
<td>1e-04*</td>
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<td>0.37</td>
<td>1e-04*</td>
<td>0.56</td>
<td>1e-04*</td>
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<td>Site 3</td>
<td>0.34</td>
<td>1e-04*</td>
<td>0.36</td>
<td>1e-04*</td>
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</table>
Figure 7: A PCoA ordination plot of both Control and Garden samples from multiple sampling Dates. Bray-Curtis Dissimilarity indices were plotted in space representing relative relatedness in species composition of the fungal communities in ginseng garden soil samples from multiple sampling dates collected from fall 2018 to fall 2020 inclusive. Data was collected from three independent garden sites.
Figure 8: Changes in Shannon Diversity (H’) and Chao1 Richness over time. Control (red) and Garden (teal) soil samples’ average Shannon diversity indices (a) and Chao1 Richness indices (b) over the first two years of ginseng cultivation from three independent ginseng garden sites. Data points are the average of 5 replicates (*except Garden samples from Summer 2020, Sites 2 and 3 which have 3 replicates). Grey bands indicate the 95% confidence interval.

In a separate PERMANOVA analysis, the Bray-Curtis Dissimilarity indices of Garden and Control samples were compared to assess if there were significant differences in the beta diversity, or the amount of community differentiation, between Garden and Control samples at each sampling date independently (Table 8). The beta diversity between garden and control samples was significantly different at less than half of the sampling dates, indicating that the presence of ginseng plants influences, to some degree, what
changes are taking place, but are unlikely to be the cause of the distinct sinusoidal patterns observed over time (Figure 8). The minimal, and inconsistent, impact of the presence of ginseng is likely due to the relatively small size of the plants and roots on the mycobiome present during the first two years of cultivation. First year ginseng roots are approximately 1 inch long, and ¼ inch wide. By the third year roots reach a marketable size and are approximately 3-8 inches long and ¼ to 1 inch thick depending on the shape and forking of the root (Harrison et al., 1992). In other words, the impact of smaller roots is likely below the detection threshold when measured in bulk soil (Dong et al., 2018). A study from 2018 demonstrated that there were significant differences in the species composition of the ginseng root rhizosphere microbiome in 2-year-old seedlings, the same age the ginseng plants were when this project concluded, compared to 3- and 4-year-old plants, demonstrating the age of the plants affects their influence on the soil microbial communities (Dong et al., 2018). This leads me to predict that as the plants in the present study of ginseng gardens continue to grow, so will their ability to influence the microbiome in the rhizosphere, and potentially into the bulk soil, which was sampled here. Sampling began in fall of 2018 after ginseng had been seeded in newly planted ginseng gardens, so rhizosphere soil sampling was not possible. Over the first two years of cultivation, ginseng roots begin to develop but remain small in size. For consistency, bulk soil samples continued to be collected and used for this project. Additionally, future diagnostic tests that aim to detect and assess GRD in potential in soil with an unknown ginseng cultivation history will be required to work effectively on bulk soil. Therefore, characterizing the bulk soil mycobiome changes was preferred over rhizosphere samples.
Table 8: P values from a PERMANOVA analysis of Bray-Curtis Dissimilarity indices comparing Garden and Control samples. Garden and Control ginseng garden soil samples’ Bray-Curtis Dissimilarity indices were compared from each individual sampling Date and garden Site. Asterisks denotes significant differences between the relative species composition of Garden and Control samples, *p<0.05.

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<tr>
<th>Site</th>
<th>Fall 2018</th>
<th>Spring 2019</th>
<th>Summer 2019</th>
<th>Fall 2019</th>
<th>Spring 2020</th>
<th>Summer 2020</th>
<th>Fall 2020</th>
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<tr>
<td>Site 1</td>
<td>0.04*</td>
<td>0.23</td>
<td>&lt;0.01*</td>
<td>0.70</td>
<td>0.09</td>
<td>0.05</td>
<td>0.02*</td>
</tr>
<tr>
<td>Site 2</td>
<td>&lt;0.01*</td>
<td>0.11</td>
<td>&lt;0.01*</td>
<td>0.15</td>
<td>0.03*</td>
<td>0.33</td>
<td>0.01*</td>
</tr>
<tr>
<td>Site 3</td>
<td>&lt;0.01*</td>
<td>0.11</td>
<td>0.01*</td>
<td>0.12</td>
<td>0.85</td>
<td>0.80</td>
<td>&lt;0.01*</td>
</tr>
</tbody>
</table>

Previous ginseng garden microbiome analyses determined and compared microbiome diversity and richness by sampling at most once per year, and the consensus was that alpha diversity significantly decreased under ginseng cultivation (Dong et al., 2018; Dong et al., 2017; Tong et al., 2021). By sampling multiple times per year, the data reported here uncovered a previously undocumented sinusoidal pattern for both diversity and richness in garden and control samples (Figure 8). Both diversity and richness in garden and control samples peaked in the beginning of first growing season, spring of 2019, and were lowest at the end of the first growing season, fall of 2019 and spring of 2020 (Figure 8). While seasonal fluctuations can greatly influence microbiome composition (Koyama et al., 2017), diversity and richness measurements in this study did not show a significant pattern that corresponded to season. However, the sinusoidal pattern in my data may have been influenced by other unpredictable weather patterns such as the amount and timing of precipitation during each growing season. For example, in the spring of 2019, when diversity was highest (Figure 8), there was a greater amount of precipitation compared to spring of 2020 (Appendix C), when diversity was lowest (Figure 8).

It will be necessary to continue tracking diversity and richness parameters throughout the next two years of cultivation in these gardens (i.e., up until harvest) to determine if the
sinusoidal trends in both diversity and richness continue. It will also be necessary to determine what may be driving this trend (if it persists) and whether an overall increase or decrease in fungal diversity and richness occurs throughout the entirety of ginseng cultivation, and whether differences between control and garden sites become consistently (and significantly) different. Regardless, when any given collection time from 2019 is compared to the corresponding collection time in 2020 (excluding Fall 2019 and 2020), a decrease in both diversity and richness become apparent. For the Fall 2019/Fall 2020 pair, an increase in both diversity and richness is apparent. As previously mentioned, many studies have reported an overall decrease in fungal diversity during ginseng cultivation (Wei et al., 2020; Dong et al., 2017), while others have reported an increase (Dong et al., 2018). It is possible that sampling time had influenced these conclusions since my project highlights some unique dynamics in the soil mycobiome in ginseng gardens and the importance of sampling time in understanding changes observed.

3.3 Relative Abundance of Fungal Species

To try and better understand the changes in the mycobiome in ginseng garden soils, 52 of the top 100 most abundant OTUs from all samples were identified and their relative abundances compared (Figure 9). The 52 OTUs were chosen as they were identified at the species level and could therefore provide the most biologically significant information. Among these identified species Gibellulopsis serrae, Humicola olivacea, Botryotrichum spirotrichum, Tricholadium griseum, Fusarium oxysporum and Fusarium solani were the most abundant. Fusarium oxysporum is a known pathogen of ginseng (Punja, 1997) found in most GRD gardens, and is often found in soils of other crops that experience replant disease as well such as Rehmannia glutinosa (Wu et al., 2015) and apple (Radl et al., 2019). While the presence of F. oxysporum in ginseng gardens was expected, its relatively high abundance from fall of 2018 onwards was surprising as ginseng plants had not yet germinated, let alone become diseased.

The relative abundance of most of the 52 fungal species tracked in Table 9 either stayed consistent throughout cultivation or showed similar patterns of change in both Garden
and Control samples. Consistent with diversity and richness analyses, this suggests the presence of ginseng had little influence on the most abundant species in the mycobiome. No species distinctively increased in abundance over time exclusively in garden soils or control soils (Figure 9). Species that show increased abundance only in Garden samples may be characteristic of GRD-induced changes, and species that increase abundance only in Control samples suggests the presence of ginseng may also resist changes driven by other shared factors. While no examples of this were identified in this study it is possible that some of the species included here will show evidence of ginseng related changes as the roots continue to mature and extend their effects further into the bulk soil.
Figure 9: Changes in the relative abundance of fungal species throughout the first two years of ginseng cultivation. Analysis of the relative abundance of 52 out of the top 100 most abundant species from all Treatments and garden Sites. A = Site 1, B = Site 2, C= Site 3, and Green = Garden samples, Orange = Control samples.
Figure 9 continued

B.

- 'Rhizopus oryzae'
- 'Umbelopsis dimorpha'
- 'Mortierella alpina'
- 'Linnemannia elongata'
- 'Salicococcus terreus'
- 'Saitozyma podzolica'
- 'Ganoderma leucocontextum'
- 'Conocybe apala'
- 'Geastrum morganii'
- 'Peziza domiciliana'
- 'Sclatidium lignicola'
- 'Pseudogymnoascus roseus'
- 'Chrysosporium pseudomerdarium'
- 'Exophiala equina'
- 'Penicillium decumbens'
- 'Penicillium jensenii'
- 'Sagenomella oligospora'
- 'Talaromyces trachyspermus'
- 'Talaromyces angelicus'
- 'Herpotrichia juniperi'
- 'Pyronochaetopsis leptospora'
- 'Pseudocoleophoma polygonicola'
- 'Murispora cicognianii'
- 'Neosetophoma rosigena'
- 'Nothophoma macrospora'
- 'Epicoccum nigrum'
- 'Epicoccum proteae'
- 'Curvularia inaequalis'
- 'Bipolaris sorokiniana'
- 'Alternaria alternata'
- 'Alternaria chlamydosporigena'
- 'Gibellulopsis serra'
- 'Coniochaeta acaciae'
- 'Chloridium asperatum'
- 'Zopfiella marina'
- 'Chaetomium afrophilum'
- 'Humicola olivacea'
- 'Botryotrichum spirotrichum'
- 'Dichotomopilus subfunicola'
- 'Trichocladium griseum'
- 'Podospora bulbilosa'
- 'Triangularia phialophoroides'
- 'Acremonium persicinum'
- 'Trichoderma hamatum'
- 'Metarhizium robertsii'
- 'Striaticonidium brachysporum'
- 'Clonostachys rosea'
- 'Gliomastix polychroma'
- 'Fusicola septimanfinisciensiae'
- 'Fusarium oxysporum'
- 'Fusarium solani'
- 'Fusarium algeriense'
Figure 9 continued

C.

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Research similar to the present study has attempted to characterize the mycobiome in ginseng garden soil using NGS, yet a clear set of taxa responsible for the development of GRD have not been identified, and the findings lack consistency. For example, Dong (et al., 2016) reported *Myrmecridium, Phaeosphaeria, Fusarium*, and *Phoma* as the primary genera that increased in abundance throughout ginseng cultivation and showed a positive correlation with diseased plants. By contrast, the same author in another study (Dong et al., 2017) found the relative abundance of *Cantharellales, Dendryphion, Fusarium*, and *Chytridiomycota* increased exclusively in ginseng cropping soils. While these two studies used very similar methods they found very little overlap in the taxa that changed significantly, and the direction of change, throughout ginseng cultivation.

Another discrepancy apparent in the NGS data published to date is the apparent absence of individual species that are known ginseng pathogens and have been suggested to have a causative role in GRD, such as *Pythium irregulare* and *Ilyonectria mors-panacis*, (Reedeler & Brammall, 1994; Hill & Hausbeck, 2008; Farh et al., 2018). *Ilyonectria mors-panacis* specifically has been proposed as the main causative agent of GRD, and yet is absent in many ginseng garden mycobiome studies. In this study *Ilyonectria mors-panacis* was identified as an OTU (Figure 10), but only contributed 0.02% to the total relative abundance and 0.26% to the total relative frequency (Table 9). Its presence does spark interest however, especially if it shows a significant increase in the abundance in bulk Garden soils in the future. Another surprising pattern of species change during ginseng cultivation is the finding that *Alternaria* species were enriched in GRD-affected soil (Wei et al., 2020) despite previous findings that reported ginsenosides are fungitoxic to *Alternaria* species (Nicol et al., 2002). Therefore, a decrease in abundance of *Alternaria* spp. would be expected throughout ginseng cultivation.

One possible explanation for the phenomena described above is that GRD does not arise from a specific shift in species profile, but rather a shift in the ratio of functional groups of microbes present in the soil (Bain et al., 2020). An increase in the ratio of pathogenic individuals to beneficial individuals can decrease the rate of essential ecosystem
functions, such as soil carbon sequestration and nutrient mineralization, and therefore decrease the ability of the soil microbiome to support plant growth (de Vries et al., 2018). For example, a decrease in the abundance of genes coding for phenolic allelochemical degradation, nutrient sensing, and uptake has been found in apple replant soils, which likely implies a decrease in the abundance of species able to perform these functions, and results in an overabundance of allelochemicals (Radl et al., 2019). This ratio of harmful to helpful taxa can be influenced by abiotic factors, such as water availability, pH and the presence of phytochemicals including ginsenosides (de Vries et al., 2018).
Table 9: The relative abundance of soil borne plant pathogens in ginseng garden soil over time. Numbers indicate the relative abundance of pathogenic taxa identified from soil samples from ginseng garden sampling Site 1 (A), Site 2 (B) and Site 3 (C). Colour intensity also reflects the relative abundance of the associated species; white indicates species was not detected or were detected in very low abundance (* indicates not detected at all) and dark green indicates the species was present in $\geq$ 3.0 relative abundance.

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Wagg \textit{(et al., 2019)} provides an excellent explanation of how important it is for microbiomes to have high diversity and richness and how this is linked to higher complexity in the functionality of the microbiome and productivity where productivity is described as the ability of the soil environment to support plant growth. Microbiomes are structured communities that function as a collective to facilitate nutrient cycling with direct feedback effects on ecosystems. Any influences that disrupt the balance or composition of the microbiome have the potential to impact nutrient cycling efficiency, and therefore soil productivity \textit{(Aremu et al., 2017)}. Characterizing the specific changes in the relative abundance of species can provide more insight into the functional changes that are occurring within the soil mycobiome \textit{(Torsvik & Øvreås, 2002; Wagg \textit{et al.}, 2019)}. Molecular phylogenetics, functional genomics, metabolomics and in situ activity measurements are also used to evaluate and predict functional roles of microbial species \textit{(Torsvik & Øvreås, 2002; DesRochers, \textit{et al.}, 2020)}. Microorganisms present in soil have many essential roles such as decomposing organic matter to release available nutrients back into the soil, holding water, inter- and intraspecies signaling, molecular transport and more \textit{(Wagg \textit{et al.}, 2019)}.

Determining the functional role of a species in a specific community can be difficult as many species have the ability to perform many different functions which can be stimulated or suppressed through feedback from the soil ecosystem \textit{(Luo \textit{et al.}, 2019)}. A microbiome with greater species richness and diversity provides a greater buffer against sudden changes in soil properties due to functional redundancy where functional redundancy is described as the presence of several taxonomically distinct species that perform the same energy-yielding metabolic functions \textit{(Louca \textit{et al.}, 2018)}. Microbial species often have several roles that directly or indirectly contribute to nutrient cycling, and these roles overlap, meaning several species can provide the same, or very similar, function \textit{(Wagg \textit{et al.}, 2019)}. Functional redundancy protects the microbiome’s ability to function well even when certain taxa are influenced by a stressor. Microbiomes with lower diversity and richness are more sensitive to ecosystem disruptions, and lower functional redundancy means they are at risk for loss of plant diversity, productivity, nutrient cycling and retention, and carbon allocation \textit{(Wagg \textit{et al.}, 2019; Hu \textit{et al.}, 2020)}. 
Long-term monoculture is known to decrease crop yields in ginseng gardens as well as most agriculture systems including cucumber (Yao et al., 2006), soybean (C. Li et al., 2010), coffee (Zhao et al., 2018), and black pepper (Cerkauskas, 2017). Monoculture is often found in parallel with decreasing soil bacterial and fungal diversity and richness regardless of what crop is being cultivated (Yao et al., 2006; C. Li et al., 2010; Xiong et al., 2015; Dong et al., 2016; Zhao et al., 2018). This phenomenon of long-term monoculture negatively impacting the microbiome composition is becoming increasingly evident as NGS studies are able to detect and characterize changes in specific microbial species (Dong et al., 2016; Zhao et al., 2018). Taxa with antagonistic abilities, such as Proteobacteria and their ability to suppress Rhizoctonia disease, are often found to decrease in abundance in soil with monocultured plant species, and common root pathogens, such as Fusarium spp. and Phytophthora spp. are usually found in increased abundance in monoculture soils, which can severely impact the functionality of the soil environment (Zhao et al., 2018).

### 3.4 Abiotic Influence

Long-term monoculture can impact both biotic and abiotic soil factors which consequently can influence the fertility and productivity of soil. Other abiotic factors that can influence the microbiome composition and productivity include toxin accumulation, pH, moisture levels, and temperature, as individual species have different ranges that support their functioning (Rousk et al., 2012; Dong et al., 2018; Wang et al., 2019). For example, continuous cropping of black pepper resulted in a significant decline in pH, organic biomass, and enzymatic activities in the soil (e.g., urease, catalase and sucrase enzyme activity) (Xiong et al., 2015; Cerkauskas, 2017). Though numerous soil physiochemical properties contribute to overall soil fertility, by using enzyme activity as a measure of physiological capacity, Waldrop et al. demonstrated the ability of a soil environment to support plant growth most highly correlated with a diverse microbial community composition (Waldrop et al., 2000).
Abiotic factors can also influence plants, which can then alter the soil microbiome through plant-soil-microbial interactions (Koyoma et al., 2018). Allelopathic and autotoxic interactions have also been found to contribute to the decline of soil health in monocultures of Angelica sinensis, Lolium perenne, and Pogostemon cablin, as well as ginseng (Kraus et al., 2002; Xin-hui et al., 2015; Yang et al., 2015; M. Li et al., 2020). Ginseng seeding and seedling establishment likely act as a disrupting factor as plant roots begin to develop and enter the plant-microbe interaction network. The exudation of ginsenosides has the ability to stimulate the growth of certain ginseng pathogens and suppress other species as previously discussed, which may initiate the shift in ginseng garden soil community composition (Nicol et al., 2002; Nicol et al., 2003; Ivanov et al., 2012; M. Li et al., 2020; Luo et al., 2020). Ginsenosides, specifically a mixture of Rg1, Rb1, and Rd, can both enrich and suppress fungi and bacteria depending on the microbial species (Luo et al., 2020). Ginsenosides have the ability to mediate interactions between the plant and soil microbiome through differential utilization of carbon sources; fungal and bacterial species present in ginseng soil that can use ginsenosides as a carbon source were enriched in a study by Luo et al. (2020). With many of these enriched species being pathogenic to ginseng roots, ginsenoside presence impacts not just the microbial community, but the plant community as well. While ginsenosides have not been proven as the main causative factor in the development of GRD (Dong et al., 2018; Bain et al., 2020), the presence of ginsenosides can alter the soil environment, and therefore affect the overall health and productivity of ginseng garden soil. The top 52 most abundant taxa that were evaluated in this project vary in their potential roles in the soil microbiome (Appendix A), but so far no significant shift in the ratio of pathogenic to beneficial/neutral species has been observed. If ginsenosides ultimately drive negative changes in the composition of the microbiomes in ginseng gardens (Luo et al., 2020), it is likely that for this study not enough ginsenosides have accumulated yet. This may be due to the relatively small size of the roots and their lower ginsenoside content after only two growing seasons (compared with mature roots after four years of cultivation), to cause an identifiable shift in the microbiome profile. The influence of ginsenosides may become more evident as the plants continue to age. Currently unpublished thesis work by MSc. student Karina Kaberi at Western University supports this prediction, as her analysis of
the ginsenoside content of the same soils analyzed in this study determined ginsenosides did not begin to significantly accumulate until the last sampling date, Fall of 2020, after 2 years of cultivation.

4. Conclusion and future directions

While new oomycete-specific primers were not successfully developed in this project, the primer set developed by Riit et al. (2016) was determined to be potentially applicable for oomycete NGS. However, as DNA extraction from the bulk soil samples taken from ginseng gardens in this study did not yield an adequate amount of oomycete DNA template to be used for NGS, they were not used successfully in this study. Since any future diagnostic analysis based on PCR amplification will have to be applicable to bulk soil, DNA extraction from sandy soils should be optimized to facilitate the characterization of the oomycete microbiome. Improved DNA extraction may also reveal greater diversity by including more rare species. Primers that target the ITS2 region (Taylor et al., 2016) were used successfully to amplify fungal DNA from ginseng garden bulk soil samples, and changes in the community composition of the mycobiome were tracked from seeding to two years growth in three independent ginseng gardens in Norfolk county, Ontario. While a distinct trend in species richness and diversity was not discernible over the first two years of cultivation, beta diversity, reflecting the overall species composition of an environment, did significantly differ between sampling dates. While the taxa present in the gardens consisted of an even mixture of pathogens and saprotrophs, the detection of known GRD-related fungal pathogens such as Ilyonectria mors-panacis and Fusarium oxysporum presents the opportunity for a shift in the balance of pathogens and saprophytes to occur in the future. During the first two years of cultivation, ginseng seedlings remain quite small and therefore their influence has likely not yet extended into bulk soil. It is important to continue sampling these ginseng gardens multiple times per year to identify key shifts in the mycobiome and track when and how they occur. Integration of fungal, oomycete and bacterial microbiomes could also reveal biotic community patterns specific to ginseng gardens soil. Luo et al. (2020) found that
the bacterial species suppressed by ginsenosides showed the greatest antagonistic abilities against enriched fungi in ginseng soil. Relationships between bacteria and fungi are critical in shaping the microbiome (Wargo & Hogan, 2006) and they can interact through numerous outlets including antibiosis, signaling molecules, chemotaxis, protein secretion and more, which highlights the need for a greater understanding of how different communities interact in the soil environment (Frey-Klet et al., 2011; S. Li et al., 2006; Legrand et al., 2017). If ginsenoside content is continually measured in these ginseng gardens, the correlation between ginsenoside accumulation and microbiome composition should also be assessed. Identifying specific compositional shifts in the soil microbiome, as well as the corresponding changes in the abiotic soil environment, could aid in the development of a diagnostic tool to determine if a potential gardens’ soil is suitable for ginseng cultivation in the future. It could also contribute to future research with the aim of mitigating GRD by identifying time-specific shifts in the soil environment that could serve at treatment targets.
References


Appendix A: Taxonomy associated with each retained OTU from all ginseng Sites, and both Treatments, and across all sampling dates.

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<th>OTU</th>
<th>Phylum</th>
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<th>Order</th>
<th>Family</th>
<th>Genus</th>
<th>Species</th>
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Appendix B: A&L Canada Laboratories Inc. soil test results.

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<th>Site</th>
<th>Organic Matter</th>
<th>Phosphorus</th>
<th>Bicarb</th>
<th>K ppm</th>
<th>Mg ppm</th>
<th>Ca ppm</th>
<th>Na ppm</th>
<th>Al ppm</th>
<th>pH</th>
<th>CEC meq/100g</th>
<th>% K</th>
<th>% Mg</th>
<th>% Ca</th>
<th>% H</th>
<th>% Na</th>
<th>Saturation % P</th>
<th>Saturation % Al</th>
<th>K/Mg Ratio</th>
<th>ENR</th>
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<td>Site 1</td>
<td>1.6</td>
<td>134 H</td>
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<td>397 H</td>
<td>169 M</td>
<td>168 0 M</td>
<td>16 L</td>
<td>1379</td>
<td>7.2</td>
<td>10.9</td>
<td>5.0</td>
<td>12.9</td>
<td>76.9</td>
<td>4.6</td>
<td>0.6</td>
<td>37 H</td>
<td>0.2 G</td>
<td>0.39</td>
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<td>Site 2</td>
<td>2.4</td>
<td>85 H</td>
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<td>236 H</td>
<td>208 H</td>
<td>900 M</td>
<td>15 M</td>
<td>1133</td>
<td>6.8</td>
<td>8.0</td>
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<td>21.6</td>
<td>56.1</td>
<td>14.7</td>
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<td>27 H</td>
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<td>Site 3</td>
<td>1.1</td>
<td>91 H</td>
<td></td>
<td>262 H</td>
<td>98 M</td>
<td>134 0 VH</td>
<td>17 M</td>
<td>1310</td>
<td>7.3</td>
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<td>20 H</td>
<td>0.2 G</td>
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Appendix C: Monthly climate data from the Delhi, ON (CDA) Ontario Weather Site. Fall is represented by the month of September data, Spring is represented by the month of May data and Summer is represented by the month of July data. Data was taken from the Government of Canada Environment and Natural Resources website under Daily Data Reports.

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<th>Fall 2018</th>
<th>Spring 2019</th>
<th>Summer 2019</th>
<th>Fall 2019</th>
<th>Spring 2020</th>
<th>Summer 2020</th>
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<tr>
<td><strong>Highest Temperature</strong></td>
<td>14.0 °C</td>
<td>19.2 °C</td>
<td>28.0 °C</td>
<td>23.6 °C</td>
<td>18.4 °C</td>
<td>29.3 °C</td>
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<td><strong>Lowest Temperature</strong></td>
<td>4.9 °C</td>
<td>6.6 °C</td>
<td>16.1 °C</td>
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<td>17.1 °C</td>
<td>12.1 °C</td>
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<td><strong>Average Temperature</strong></td>
<td>9.4 °C</td>
<td>12.9 °C</td>
<td>22.0 °C</td>
<td>17.0 °C</td>
<td>12.3 °C</td>
<td>23.2 °C</td>
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<td><strong>Total Monthly Precipitation</strong></td>
<td>112.9 mm</td>
<td>100.4 mm</td>
<td>121.4 mm</td>
<td>54.9 mm</td>
<td>46.6 mm</td>
<td>54.5 mm</td>
<td>50.9 mm</td>
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Appendix D: Alpha rarefaction curve using Shannon diversity. A maximum sampling depth of 15,000 was chosen as it was approximately the median frequency per sample.
# Curriculum Vitae

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<tr>
<th>Name:</th>
<th>Megan Lambert</th>
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| **Post-secondary Education and Degrees:** | The University of Western Ontario  
London, Ontario, Canada  
2014-2018 B.Sc.  
triOS College  
London, Ontario, Canada  
2020 Phlebotomy Certificate  
The University of Western Ontario  
London, Ontario, Canada  
2018-2021 M.Sc. |
| **Honors and Awards:** | The Western Scholarship of Distinction  
2014  
Dean’s Honor List  
2016-2018 |
| **Related Work Experience:** | Teaching Assistant  
The University of Western Ontario  
2018-2020  
Microbiology Laboratory Technician  
A&L Canada Inc.  
London, Ontario, Canada  
2021 - Present  
Society of Biology Graduate Students  
The University of Western Ontario  
London, Ontario, Canada  
2018-2020 |