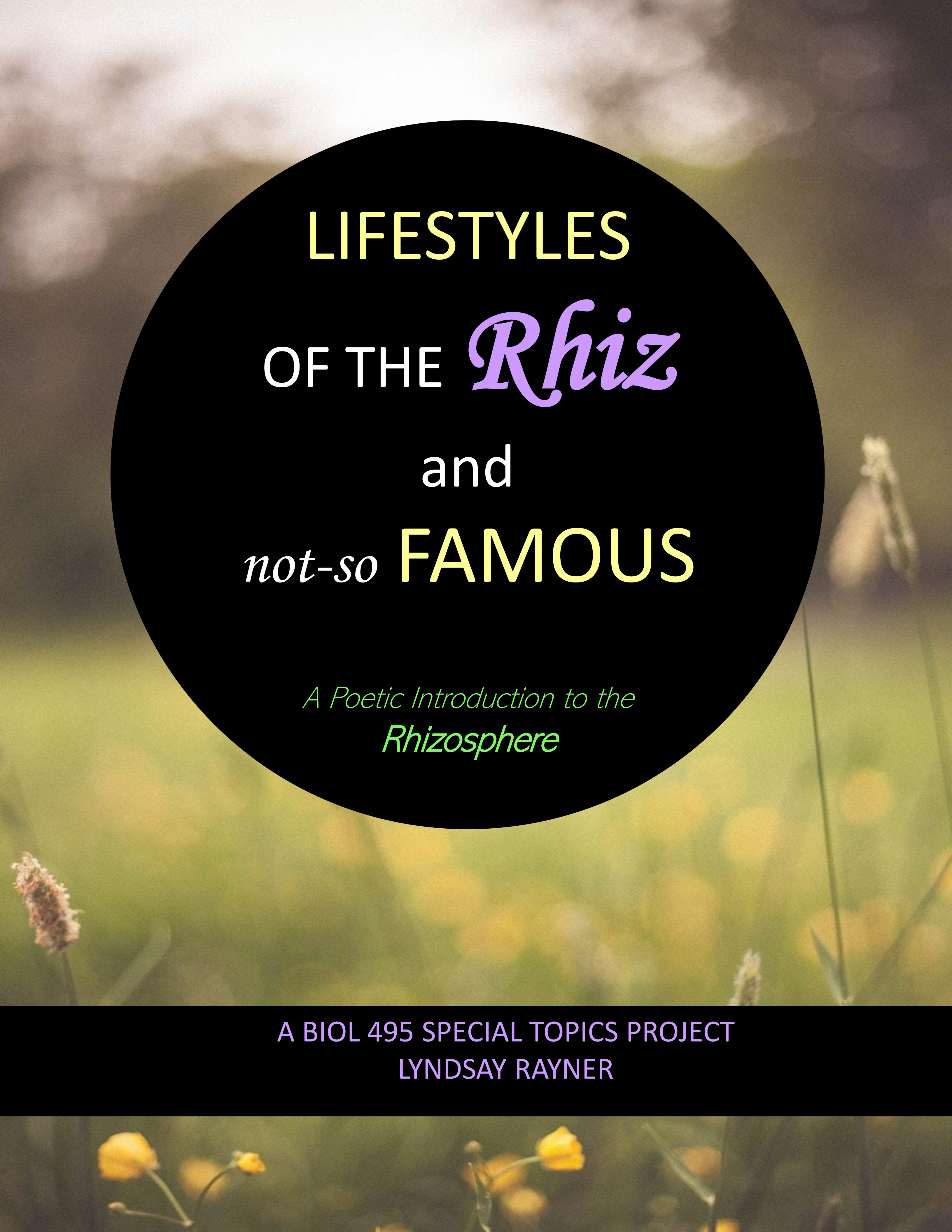

LIFESTYLES OF THE *Rhiz* and *not-so* FAMOUS

A Poetic Introduction to the ***Rhizosphere***

A BIOL 495 SPECIAL TOPICS PROJECT

LYNDSAY RAYNER

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Vol. 4(1) | DOI: https://doi.org/10.31542/muse.v4i1.1867
MacEwan University Student eJournal | © 2020 under CC BY-NC | ISSN 2369-5617

hello,

Welcome to a poetic introduction to the rhizosphere! This small book was created to share and explore the fascinating world that exists below the ground. If you are already someone with a special interest in botany, agronomy, microbiology, or ecosystem ecology in general, this is for you! And if you do not have much knowledge in any of these areas, the information within the following poems and supporting pages will help you gain an understanding and appreciation for this interesting environmental niche.

The rhizosphere is a dynamic place where plant roots interact with soil, along with all of the living things that occupy this very small, yet very important space. Plants are often viewed as the foundation sustaining all living things on terrestrial Earth. But what about the components that sustain and impact our beloved chlorophyll companions? What helps them thrive? Where do the nutrients come from? What may potentially harm them? This collection of poems will help shine light onto the essential role that the microbial community plays on plant life and ecosystems at a global level.

I hope you enjoy reading and learning about this amazing microbiome.

Welcome to the Rhizosphere

Let’s go on an adventure to one of the most diverse places on Earth,
No, it is not the ocean, the tropics, nor the coastline of Perth.
We’re going to the microscopic world where soil gives birth.

This place is vital, the origin of our terrestrial food source.
A dynamic dance of roots moving through soil with such force.
Why, it’s the remarkable rhizosphere, of course!

It can not be defined by size, structure or shape,
Rather by a chemical gradient, a very complex landscape.
With so much more to discover, the surface has only just been scraped.

The microbial populations are so inconceivably high:
Streptomyces, pseudomonas, and also, symbiotic fungi.
Though, anthropogenic practices may be harming the supply.

Conventional agriculture tends to ignore the health of the land.
Clear cutting, tilling, and spraying chemicals - all getting out of hand.
Permaculture and regenerative farming is what consumers must demand.

The diversity in the soil depends on the diversity of the roots,
but with monoculture crops, the healthy assortment dilutes.
Intercropping and yearly rotations would lend better attributes.

The roots of the plants have more than one single mission,
They absorb, they anchor, and grant rhizobia permission.
They also feed many organisms, thus, the high rate of competition.

But sadly, this precious microbiome is quite often ignored;
The world above ground is much more thoroughly explored.
Perhaps scientists and researchers should be offered more of a reward.

The rhizosphere is crucial for all of life, that's confirmed.
Many interactions and relationships have already been observed,
But there is definitely still so much more to be learned!

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NUTRIENT STARVED SAPLING

Many have studied and pondered
the idea of altruism in nature:
Ground squirrels producing risky calls,
and Emperor penguin moms embarking on dangerous fishing hauls.
Sure, some animal parents sacrifice and risk for their offspring,
but in the kingdom of plants, could this also be a thing?

Does anyone hear me, **a young sapling**, and my chlorophyll plea?
Would my parents do anything to ensure I succeed?
Perhaps not the ultimate sacrifice, but what about just to share -
extra carbon, for their weak and quite vulnerable heir.

Animal behaviour is much easier to study,
Because us plants are not conscious, to think that would be nutty.
Plus, there are other organisms acting upon us, altering our behaviour.
Like Ectomycorrhizae, a true forest savior!
To me, a young Douglas fir, mycorrhizae is my friend,
increasing nutrient uptake and making my roots extend.
My infancy was a struggle,
nitrates and phosphates, I could not smuggle.
My primary root grew and stretched,
but failed to retrieve water from the deep soil depths.
I needed some help, I needed some assistance,
I signal my long-time pal to provide sustenance.
My roots send out strigolactones, a special invite
to grace my cells with a Hartig net, such a delight.
Forging a way through the tangle of underground traffic,
multiplying chitin and extending hyphae, so dramatic.

Over evolutionary time we become fluent in this biochemical speech
for mutual benefits: you receive carbon, and I gain your reach.
You also make a connection between the other woody plants,
Creating a source-sink relationship, allowing the weak to enhance.
You help me grow tall, but I know there will come a day,
when I too, will share my hard earned photosynthate.

M mycorrhizae, from the Greek words meaning fungus and root

O obligate symbionts depend completely on plants for carbon

T terrestrial plants first forming mycorrhizal relationships 400 million years ago

H hyphal network connecting many plants within a community

E extra carbon-based photosynthates feed the mycorrhizal fungi

R root exudates containing strigolactones initiate the relationship

T transfer of carbon isotopes suggest the possibility of kin recognition

R relatedness of trees may influence the allocation of transferred carbon

E ecto prefer woody trees and the intercellular spaces of roots

E endo are found with most angiosperms and create intracellular arbuscules

Roses are red, violets are blue,
the Rhizosphere stops before
the vascular tissue

Methods are read,
Results have been viewed,
P-value is less than alpha,
so we can significantly
conclude

Gram-negative appear red,
Positive, more blue,
Some bacteria can produce
antibiotics to better protect
you!

The data have a normal spread,
equal variation's been proved,
Random and independent
samples are also assumed

Biodiversity of the Soil

To many, soil is boring, just a place to build your deck.
To cleaners and maids, dirt's an utter pain in the neck.

But it's more than just filth, it sustains the whole planet
From apples and almonds to parsnip and pomegranate.

It's comprised of many things, more than an amalgamation of minerals
Bacteria, microbes, and fungi present at various intervals.

An abiotic medium, chalk-full of living creatures
Can decompose and create nutrients, among other features.

The organisms, so condensed, hopefully none have claustrophobia
Including the legume-loving and nitrogen-fixing rhizobia.

And then there's the fungi that connect so many plants
Sharing carbon and nutrients, giving saplings a fighting chance.

This mycorrhizal network is often viewed as beneficial,
But it can be detrimental to some, not always fair and judicial.

The genus *Pseudomonas* is important for plant growth and protection,
But some strains increase susceptibility of pathogen infection.

The interactions are complex, and vary with species or association,
Mutualistic or parasitic, it all depends on the situation.

Fusarium oxysporum: a biocontrol agent causing weed cessation
But, simultaneously destroying the cereal crop population.

Another vast group of organisms, they mitigate abiotic stress,
These plant growth promoting rhizobacteria add much to plant success.

They increase root biomass and phosphorous availability,
Even encourage defensive phytohormone capability.

Now, moving up in body size are the highly diverse nematodes.
This vast phylum of microfauna affect soil by several modes.

Some are herbivorous and thus damage the plant's condition,
While others feed on bacteria and fungi aiding in decomposition.

So now it is clear, there is much biota that make up the soil.
And it's all due to the root exudates, the fuel for this turmoil.


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Bt

An innocent little soil dweller, just minding its own business,
but causing quite the controversy, it is *Bacillus thuringiensis*.
This naturally occurring soil bacteria has a very special trait,
a toxic crystal protein causing some insects to meet their fate.
With advances in genetic engineering, this feature has been transferred
into the DNA of plants - lines of nature now seem blurred.
Some people think this manipulation is wrong and offensive,
but it has made agricultural crops more robust and defensive.
The need for chemical pesticides has also been reduced,
even with poor conditions more food can be produced.
But the public opinion is not very fond of GMOs;
they’re worried of ecological side effects and growing 11 toes.

The benefits have been shown, we can feed many more humans,
but even meta-analyses come to undecided conclusions.
These studies investigate disruptions in soil enzyme activity,
and warn that alterations can signal a reduction in edaphic fertility.
With long-term consequences still largely unclear,
we will just have to keep researching year after year.
Evaluating effects of the toxic Cry1Ab protein
and observing changes emerging in the rhizosphere scene.

Give Peas a Chance

Legume plants deserve a whole lot of appreciation
They form bonds with bacteria, a very special relation.
The bacteria *Rhizobium leguminosarum* have an important occupation:
They're able to perform energetically expensive nitrogen fixation.
This ability allows soil to remain full of nutrition
That's why legumes are so often used in a farmer's crop rotation.
This practice improves yields, combating global starvation,
Allowing producers to grow healthy food for the next generation.

But the forming of this partnership is quite a complex situation.
Flavonoids and nod-factors are the modes of communication.
When the signal is received, plant root hairs undergo deformation,
it curls around the bacterium, forming a cozy insulation.
The small space is now anaerobic, a place of salvation,
And the bacterium can now grow its long thread of infection,
Spreading through the plant, undergoing proliferation,
The multiplying bacteria eventually form visible nodulation.
The *Rhizobium* convinces the plant it's a friendly invasion,
Because this symbiosis is mutual, quite a remarkable adaptation

A Critical Assessment

These poems were not made simply for entertainment,
they're backed up by research to support every statement.
But before any claims or conclusions can be made
evidence of following the scientific method must be displayed.
With so many researchers rushing to publish,
a surprising number of articles are actually pure rubbish.
Mistakes and flaws are often found in the stats
or standard error bars misrepresented on graphs.
When doing parametric tests, all of the assumptions must be met;
a normal distribution is one you should never forget.
Samples should be independent, and strong correlations more linear,
there's the option for non-parametric, but those tests may be inferior.
It's hard to believe some papers are even peer-reviewed,
perhaps the reviewer's names should always be debuted.
And then there's the issue of predatory journals;
purely in it for the money, making authors jump over hurdles.
Only to discover the editing process is weak, not robust.
These cases lead scientists and students to develop mistrust.
To highlight this issue, John Bohannon conducted an operation.
He submitted papers and was published with totally phony information.
Some of these journals have been collected and publicly shamed,
thanks to Jeffrey Beall's list some scientific rigour has been regained.
Now that it's been shown that published papers can be fraudulent,
As future or current scientists, we must always stay vigilant!

Background and Information: Lifestyles of the Rhiz and Not-So Famous

Lyndsay Rayner

Welcome to the Rhizosphere

All of terrestrial life relies upon plants; they are the primary producers of Earth. Not only are they the base of the food chain, sustaining all organisms up to the highest trophic levels, they are able to sequester toxins from the ground, act as a carbon sink, and provide habitats for animals and the raw materials for humans. For being so fundamental in the survival of terrestrial organisms, we have previously overlooked one of the most significant drivers controlling plant processes. This place is the rhizosphere: the microscopic area where soil and plant roots interact (Morrissey et al. 2004, Hinsinger et al. 2009). Soil is unique in that it is an ecosystem factor comprised of both abiotic and biotic components. This medium contains rock minerals and water, as well as both living and dead organic matter. The bulk soil is often limited in nutrients; however, the small area within the rhizosphere is an extremely biologically and chemically diverse place. It's the plant roots that exude an array of chemicals and carbon-based molecules and deposits that provide the rich source of energy for soil swelling microbes and micro fauna (Essarioui et al. 2016). This densely populated microbiome results in an endless number of interactions, both cooperative and competitive, among the plant, bacteria, fungal, and animal species (Hinsinger et al. 2009, Essarioui et al. 2016).

To keep up with the growth of the human population, agricultural productivity also needs to increase. While conventional agriculture provides efficiency and high yields, we are also seeing negative consequences such as loss of biodiversity, reduction in soil fertility, and eutrophication from fertilizer runoff (Morrissey et al. 2004, Ren et al. 2020). Today, the majority of crops are grown as monocultures with the use of chemical pesticides, synthetic fertilizers, and on tilled land, all of which impact rhizosphere processes and the health of soils (Morrissey et al. 2004). A higher diversity of soil microorganisms has a positive impact on plant health, and the diversity of bacterial and fungal communities have shown to be highest in soils that are untilled and retain the stubble of previous crops (Essel et al. 2019). Leaving the roots of stubble intact allows for plants to decompose naturally, returning nutrients to the soil. Additionally, when soil is undisturbed, the sequestered carbon remains underground rather than being released back into the atmosphere (Essel et al. 2019, Hinsinger et al. 2009). The use of intercropping, cover crops, and crop rotations all aid in retaining soil moisture and nutrients, making it a more hospitable environment for microorganism and plants alike (Essel et al. 2019).

Nutrient Starved Sapling

There are several examples of altruism within the animal kingdom. This occurs when an individual sacrifices or puts themselves at risk for the sole benefit of others. It is sometimes hard to decipher if the actions are conscious decisions or unconscious instincts, but many of these incidences occur between parents and their offspring (Dugatkin 2014). The idea that plants may

Vol. 4(1) | DOI: https://doi.org/10.31542/muse.v4i1.1867
MacEwan University Student eJournal | © 2020 under CC BY-NC | ISSN 2369-5617

preferentially share resources with those closely related to them was proposed by researchers looking at the underground mycorrhizal network that connects trees in the boreal forest (Pickles et al. 2017). Ectomycorrhizal fungi (EMF) form connections with the roots of many species of woody plants. The fungus plays a role in nutrient cycling within the soil but is also suggested to mediate carbon transfers among species. Additionally, Pickles et al. (2017) hypothesized that the EMF may actively direct and target the flow of carbon to trees that are more closely related, thus exhibiting kin selection among plants. The researchers used carbon isotopes to tag and track the movement of photosynthates between trees they established to be either donors or recipients. Although an interesting concept, the ability for plants and fungi to choose where photosynthates are allocated based on relatedness was not strongly supported. The study only found a significant effect in half of the samples, as well as evidence of carbon transfer among different species. An alternative and simpler explanation is based on a source-sink relationship (Pickles et al. 2017), where the carbon gradient is influenced by environmental factors and growing conditions (Simard et al. 1997). For example, a plant exposed to ample sunlight takes on the role of a carbon source, while one in a highly shaded area would be a sink (Simard et al. 1997).

Regardless of any kinship effects among plants, what is true is that the majority of plants within a given area or community are connected through the hyphal network of underground mycorrhizae (Bonfante and Genre 2010). Although the plant-mycorrhizae relationship is often described as mutualistic, the true effects can be either beneficial, neutral, or harmful depending on the species involved, the nutrient soil content, and other biotic and abiotic factors (Francis and Read 1995, Jones and Smith 2004).

The mycorrhizal relationship is initiated by the release of strigolactones from plant roots. The strigolactones act as a chemical messenger and stimulate the fungal metabolism, producing more chitin and thus growing and extending the hyphae towards the roots. The hyphae also release chemicals, generally termed myc-factors, to which the plant responds, prepares for the fungal infection, and becomes a part of the large underground network (Bonfante and Genre 2010).

Mother Tree

Mycorrhizae comes from the Greek words for fungus and root (Harrison 2005). It has been estimated that this plant-fungal relationship has existed for over 400 million years and is exhibited among 90% of plants (Bonfante and Genre 2010).

The associations are often divided into two general categories: ectomycorrhizal fungi (EMF) and endomycorrhizal fungi. Endomycorrhizae includes other sub-categories, like the very specialized and specific relationships within the Orchidaceae and Ericaceae families, as well as the more widespread arbuscular mycorrhizae (AM), which are found connected to the roots of angiosperms (Harrison 2005). AM belong to the phylum Glomeromycota and are obligate symbionts, meaning they rely completely on their host plant for carbon, and thus are never free-living in the soil (Harrison 2005).

As previously described, the relationship is initiated by the release of strigolactones from plant roots. Strigolactones are a group of phytohormones derived from carotenoids. They are responsible for multiple physiological processes but were first discovered for their role in the germination of parasitic plant seeds, and later as an inhibitor of shoot branching (Al-Babili and Bouwmeester 2015).

In the case of EMF, these form relationships with roughly 2% of plant species, most of which are trees and other woody plants (Tedersoo et al. 2010). EMF form a sheath around the root and then grow between cellular spaces, avoiding penetration of the cell walls. The hyphae surrounding the cells create a dense mantle forming the Hartig net (Pickles et al. 2017). Alternatively, AM are much more widespread with over 70% of plant species acting as hosts (Francis and Read 1995). AM also differ in that they penetrate the root cells and produce arbuscules - fan-like branches which are the site of nutrient transfer (Harrison 2005).

Biodiversity of the Soil

Soil is not always thought of as the rich and diverse living environment that it truly is. Soils make up the largest reservoir of biodiversity on the planet and are host to a variety of archaea, bacteria, fungi, protozoa, nematodes, and other various invertebrate microorganisms (Hinsginer et al. 2009).

Pseudomonas, a genus of gram-negative bacteria, are very diverse and found in a wide range of niches. However, they are in exceptionally high abundance within the rhizosphere (Primo et al. 2019). Like all other microorganisms that converge in the rhizosphere, they are attracted to this place due to the abundance of nutrients available provided by plant roots. *Pseudomonas* can act on plants and other microbes in various ways. Strains of *P. fluorescens* are shown to benefit plants by triggering induced systemic resistance against bacterial pathogens (Haney et al. 2017). However, the effects of *P. fluorescens* can change based on variables such as the presence and degree of herbivory on the plant, as well as the activation or disruption of the defensive plant hormones salicylic acid and jasmonic acid (Haney et al. 2017).

Relative to *P. fluorescens* is *P. syringae*, a bacterial pathogen that thrives on the foliar parts of plants. These bacteria can infect over 180 plants including both agricultural crops and ornamental plants, causing much destruction as well as economical losses (Primo et al. 2019). The various consequences and outcomes show that there are always a large number of complex interactions taking place within the soil and acting on the vast diversity of organisms.

Another example of the fluctuating effects seen within the rhizosphere is with the filamentous fungi *Fusarium*. It is difficult to categorize it as either beneficial or harmful because its actions are subjective and depend on the species it interacts with. For example, some strains of *Fusarium* act as an effective biocontrol agent for noxious weeds (Kazan and Gardiner 2018). However, due to its strong herbicidal traits and the ability for the spores to lay dormant for many years, it is especially dangerous and destructive to cool temperature crops such as rye, wheat, and oats (Kazan and Gardiner 2018). Because of this, it is important to know what specific species may be more or less tolerant to this potential pathogen when considering its use as a weed controller.

Streptomyces is another common genus of soil bacteria. This genus is gram-positive and filamentous, appearing to more closely resemble fungi. *Streptomyces* are known for their impressive ability to produce antibiotics, which is important for both human health and the health of the organisms within the rhizosphere (Essarioui et al. 2016). They are found in particularly high abundance in soils with plants, especially agricultural crops as they have a potent antagonistic effect against plant pathogens. Due to their close association with plants, the majority of their energy and nutrients come from plant exudates. D-mannose and maltotriose are the compounds that are consumed in the highest quantities by *Streptomyces* (Essarioui et al. 2016).

Drought is one of the most prevalent stressors affecting plants and is especially problematic for agricultural crops. Plant growth promoting rhizobacteria (PGPR) is a generic group of bacteria categorized for colonizing plant roots and offering several benefits to the plants. Some of the ways PGPR impact plants include increasing the production of plant hormones for both defense and growth, increasing available phosphorous, increasing root biomass and expansion to gain more access to water and nutrients, affecting enzymes responsible for mitigating the harmful effects of ethylene, and also for enzymes required for nodulation of nitrogen fixation. Beyond their direct effect on plants, PGPR also help shape and improve the general quality of the surrounding soil by making it more fertile (Khan et el. 2019).

With body sizes ranging from 5-100 µm around and 0.1-2.5 mm long, nematodes are relatively large compared to other soil microorganisms. Nematodes make up the entire phylum Nematoda, and because this is such a broad taxonomical group, the functionality and impacts on the rhizosphere are equally extensive. The position a nematode has within the food web is most influential for how it will impact the environment. For example, nematodes can be bacterivores, fungivores, herbivores, and/or prey on other small animals and microfauna. The herbivorous nematodes are often categorized as pathogens due to their detrimental effects on plants, specifically the roots. Whereas those that feed on bacteria or fungi are beneficial as they aid in decomposition, resulting in more available nutrients within the soil (Geisn et al. 2018).

BT

The genetic engineering (GE) of plants and other organisms is faced with conflicting opinions from both the public and scientific communities. Genetic engineering involves the transfer of one segment of DNA (specific genes) into the genome of a separate species (Khan 2009). This alteration of DNA causes unrest among those that believe nature should not be altered in this way, and that scientists should not attempt to play God. On the other hand, with improvements in GE technology, geneticists are able to more accurately and efficiently pinpoint exact genes and effectively imbed them into foreign chromosomes (Khan 2009). One of the major benefits to GE is the ability to improve plant defenses and increase resistance to both abiotic and biotic stressors. With an ever-growing human population, the issue of food shortages is a constant concern, and only continues to worsen. With GE, plants have been developed to withstand less than optimal conditions, and have an increased resistance to pests, thus requiring less chemical pesticide inputs (Li et al. 2019).

One of the most well-known, and highly debated examples of GE is regarding the soil bacteria *Bacillus thuringiensis* (Bt). The bacteria produce a toxic crystal protein (Cry1Ab), which has been inserted into the genes of many plants, including cotton and corn. When ingested by insects, the Cry1Ab protein damages and paralyzes the digestive tract, causing the insect to eventually stop eating and starve to death. With transgenic Bt crops, the protein is systemic and resides continuously within the plant, resulting in less need to apply and spray chemical insecticides. This is both cost-effective and more environmentally friendly (Oliveira et al. 2008).

Bt only targets specific organisms, thus lowering the concern for a negative effect on humans or other animals. However, because the protein resides within the plant, it can still be released back into the soil via root exudates. Because of the concern and unknown effects Bt crops can have on the surrounding soil environment, Oliveira et al. (2008) conducted a study comparing the microbial populations within the soil of isogenic and transgenic corn plants. They concluded that Bt had no significant impact on the microbial populations, and that any changes were more likely due to seasonal differences between the two years. However, the experimental design, techniques, and approaches they used to evaluate the microbial communities were somewhat weak. This study had an unintentional sample size of one, due to all measurable units (individual plants) being planted in the same plot. They also failed to categorize the microorganisms into more specific functional groups. There have been numerous experiments and meta-analyses conducted on GE plants in an attempt to reach unified conclusions regarding this very controversial and disputed topic (Li et al. 2019).

Give Peas A Chance

Although it makes up the majority of Earth's atmospheric gases, nitrogen is one of the most limiting nutrients within soils. This is because the dinitrogen gas molecule is unavailable to plants and must be reduced into inorganic forms such as ammonium (Chapin III et al. 2011). The nitrogen fixation process can be carried out by *Rhizobium*, a genus of bacteria equipped with the nitrogenase enzyme which helps break the strong triple bonds of dinitrogen. Nitrogenase is sensitive to oxygen and will be irreversibly inhibited when exposed to oxygen gas (Chapin III et al. 2011). The nodules that *Rhizobium* form with the roots of legume plants provide a safe, anaerobic environment for the nitrogen fixation to occur.

The relationship between the plant and the *Rhizobium* begins with the plant exuding flavonoids from its roots. These compounds act as messengers which are received by the bacteria. The bacteria then release chemicals of their own (nod-factors), which are received by and cause several physiological changes within the plant (Crespi and Frugier 2009). The first transformation is to the root hairs. Once the bacteria come into contact with the root hairs, the plasma membrane depolarizes, generating a spiking calcium signal, rearranging the actin filaments near the root hair tip, eventually causing the root hair to branch out and curl under, engulfing the bacteria. Once the bacteria are integrated into the root hair, they send down an infection thread which grows and expands into several of the surrounding root cells. Both the plant cells and bacterial cells proliferate, eventually forming visible nodules. Once the nodules are formed, nitrogen fixation can occur (Crespi and Frugier 2009).

The relationship between *Rhizobium* and legume plants is considered to be mutualistic. The bacteria provide a useable source of nitrogen, and the plant provides energy in the form of photosynthates which help power the energetically expensive fixation process (Chapin III et al. 2011). *Rhizobium* not only provide a direct source of nitrogen for the plant, but also enrich the surrounding soil. This is why legumes continue to be incorporated into crop rotation practices as a way to naturally improve soil quality without relying completely on synthetic fertilizers (Morrissey et al.. 2004).

A Critical Assessment

To properly conduct research in any field, one must have a strong understanding of the scientific method, an effective and detailed experimental design, knowledge about what statistical analyses are most appropriate and how to interpret them, and lastly, the ability to communicate the results. Upholding scientific rigour is not only the responsibility of the researchers and scientists directly involved with a study, but also the editors and publishers of journals, as well as the extended scientific community reading the articles.

Professors and instructors constantly remind students of the importance of academic integrity and how an author cannot make claims without referring to scientific evidence as support. In university, students begin to understand how strict the publishing process is for scientific papers. In a shocking article by John Bohannon (2013), he describes his experience of publishing a study containing false information, and errors in both methodology and the interpretation of results. His paper uncovers the shameful truth that the world of publishing scientific papers is not always as stringent as we are made to believe. He exposes some journals for neglecting a strict editing and review process, and others for dishonesty in terms of payment. A list of these untrustworthy journals has been compiled by Jeffrey Beall and can be found here: https://beallslist.weebly.com/.

In the often competitive world of academia, there is a strong push by researchers to publish their work as soon as possible. This time constraint can lead to detrimental shortcuts during the experimental process or errors in the published document. Because of this, readers should always be critical of all claims and methods used in scientific papers. The statistical analysis, interpretation, and communication of data and results is where most of the mistakes occur (Whitlock and Schluter 2015). If readers are unsure of proper and correct use of statistical methods, they should refer to legitimate sources (Hoekstra et al. 2012).

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