RESTORATION OF A DISTURBED SEMI-ARID GRASSLAND USING PRIORITY EFFECTS AND SOIL AMENDMENTS TO PROMOTE NATIVE PLANT COMMUNITIES AND PREVENT INVASION BY EXOTIC SPECIES

by

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ABSTRACT

As an ecosystem, grasslands in British Columbia are home to a third of the province's endangered and threatened species but make up less than 1% of the total land coverage in the province. Grasslands provide numerous important ecosystem services such as carbon sequestration, hydrology control, and maintaining species diversity. Anthropogenic disturbances threaten grasslands and once disturbed are challenging to restore or reclaim. My project tests successional theory and priority effects to restore native grassland plants with different soil amendments (straw matting and biochar). Priority effects entail different seeding orders of arrival of successional plant species and may be used to determine the best combination that promotes the establishment and growth of native plant communities and prevents invasion of exotic species in grassland restoration. Combinations of four different planting orders of native early and late successional grasses and forbs, and four different soil treatments were applied at three different sites in Kenna Cartwright Nature Park in Kamloops, British Columbia, Canada. In addition, a greenhouse study was conducted using three different planting orders and two fertilizer levels to test priority effects and the resilience of a native grassland community against invasion. Results show early successional plants exhibit stronger priority effects in the greenhouse but in the field the results of priority effects are site specific. Plots in the field that received both biochar and straw matting as amendment treatments experienced higher soil moisture and less exotic invasion. These findings provide insight into the benefits of using priority effects and amendments in a restoration setting in the interior grassland of British Columbia, giving restoration managers more tools to help restore land as anthropogenic disturbance becomes increasingly more common.

Keywords: Grassland Restoration, Priority Effects, Succession, Soil Amendments, Native Plants, Exotic Species

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DEDICATION

I would like to dedicate this work to my family. Mom, Dad, Nick, and Makenzie, you have pushed me to challenge myself and always strive for better. Without your loving support over the past few years, the completion of this project would have never been.

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CHAPTER 1: INTRODUCTION

THE IMPORTANCE OF BRITISH COLUMBIA GRASSLANDS

As an ecosystem, grasslands are threatened in British Columbia, and make up less than 1% of the total land coverage in the province (Tisdale 1947, Gayton 2004). It is estimated that 35% of the remaining grassland ecosystems in British Columbia are dominated, up to 84%, by non-native herbaceous vegetation (Gayton 2004). As well as being home to one-third of the province's endangered and threatened species, grasslands provide important ecosystem services such as carbon sequestration, hydrology control, and cultural significance (Iverson 2004). Human activities such as livestock grazing, mining practices, and rapid urban development are some of the major causes of the threat to grasslands (Macdougall 2008). Degraded grasslands can be susceptible to the invasion of forbs and grasses, causing the ecosystem to convert to an alternate state ecosystem, as well as causing native populations to dwindle in size (Macdougall 2008).

Preserving grasslands is important for maintaining species diversity and numerous ecosystem services (Bengtsson 2019). Grasslands that are well managed are recognized for their biodiversity and production (Habel 2013), thus providing ecosystem services such as helping to reduce the atmospheric concentration of CO_2 through sequestration in the soil, conservation of soil, and conservation of the genetic library (Sala 1997). Biodiversity also contributes to climate regulation, aesthetic appeal, and pollination (Hanisch 2020). Therefore, grasslands are an important world ecosystem and should be protected and restored when possible. Without them we lose vital services to the world that would otherwise be impractical to replicate.

Grasslands and rangelands total value has been estimated at $232 USD per hectare per year, with a majority of that cost being derived from waste treatment (estimated value of $87 USD per hectare per year), food production (estimated value of $67 USD per hectare per year), erosion control (estimated value of $29 USD per hectare per year), and pollination (estimated value of $25 USD per hectare per year), however, these estimates do not include carbon storage or climate regulation into their assessment (Costanza et al. 1997). In British Columbia alone, there is 0.74 million hectares of grassland, which would place the estimated value of the services provided to us by grasslands at roughly $172 million USD. The world resource institute PAGE analysis of grassland estimated that carbon storage potential of grassland ranged from 650 to 810 gigatonnes of carbon per year (GtC/yr) (White et al. 2000). With this estimate, in British Columbia, there is potential for 74 million to 222 million hectares of carbon to be stored in grassland ecosystems. Based on the avoided carbon emissions into the atmosphere, the Ontario green belt study estimated the value of carbon storage per hectare to be $28.46 USD per year. If this estimate is used, British Columbia grasslands are worth $21 million USD per year for carbon storage (Wilson 2009). When the estimated total value of ecosystem services provided by grasslands in Costanza (1997) is combined with the estimated total value of carbon storage of British Columbia grasslands from Wilson (2009), the total value of grasslands in British Columbia can be estimated around $193 million USD per year. Due to inflation, we can expect the total estimate to be higher than $193 million USD per year.

The estimated total value of grasslands shows that the loss of grasslands will harm both global and local economies. If there is no global effort to help mitigate the effects of grassland loss through protection, maintenance, and restoration, then this outcome could continue to be amplified.

RESTORING AN ECOSYSTEM

Restoring an ecosystem to a target state requires guiding a disturbed ecosystem through the process of recovery, which often entails assisting ecosystems through certain successional steps (Bossuyt and Hermy 2003). It is a detailed process focused on restoring and promoting the natural diversity of flora and fauna, while also preventing the invasion of exotics, and promoting ecosystem function. Having a rapid establishment of plants through seeding is important to rebuild soil, control erosion, and to improve a degraded site's visual appearance (Burton and Burton 2006).

A classic practice of restoration is to benefit the growth of native species, while limiting the growth of exotic species (Hess 2019). The success of an invading species is based on how the invader interacts with the physical and biological characteristics of the ecosystem in which it is invading (Lonsdale 1999, Williamson 1999). Exotic species' ability to invade and sequester resources has long been considered as the determining mechanism of a successful invasion (Vila and Weiner 2004, Pyšek and Richardson 2008). It has also been suggested that invasion success is determined by resource availability (Davis et al. 2000), the native plant community present in the invaded ecosystem (Levine and D'Antonio 1999, Fridley et al. 2007) and the trophic interactions between the native species present and the invaders (Mitchell et al. 2006; Foster et al. 2021).

Ecology is focused on the distribution and abundance of organisms in a body of space over a period of time. The ability of researchers to predict the ecological, biogeographic, and climatic changes of ecosystems in response to ongoing climate change is paramount. Most challenging of all is the chance of isolated and episodic climatic events occurring more frequently. This has been proven to cause ecosystem emergencies that would be detrimental to native flora and fauna communities, while generating spikes of exotic species invasion (Suarez et al. 2004). Additionally, this would be detrimental to sensitive climatic life events of native species, contributing to the worldwide downfall and extinction of species in British Columbia, in tandem with the collapse of ecosystems (Jackson 2009).

However, successional pathways can be multi-directional, with stochastic processes and disturbances driving them (van der Maarel 1992). This implies that an ecosystem has the potential to arrive at multiple stable states with unstable transitions (Scheffer et al. 2001). The surrounding biotic factors, abiotic factors, and random organismal arrival will determine the alternative stable state in which an ecosystem arrives. The problem is that an ecosystem that has been invaded may remain in that stable state for extended periods of time (Suding et al. 2004). This information is important towards understanding when to conduct restoration research because the project cannot only be focused on arriving at a traditional steady state, but it must create a sustainable steady state that can withstand inevitable environmental changes and events. This idea will be a main concern when looking at the potential species of flora that will be used in this project.

RESTORATION USING PRIORITY EFFECTS

Priority effects occur when the arrival order and timing of plants, germination rate, and seedling rates in an ecosystem can affect long term community structure. In a newly colonized ecosystem, early successional plants that establish themselves will have a competitive advantage over plants that arrive later (Erikkson and Erikkson 1998, Sarneel 2016, Ploughe et al. 2020, Yu et al. 2020). In addition, the order and timing of these different arrivals can have a long-lasting impact on community structure, resilience, and community functioning (Fukami et al. 2010, Körner et al. 2008, Švamberková, Doležal, and Lepš 2019, Weidlich et al. 2017, Weidlick et al. 2018, Wilsey et al. 2015). Therefore, priority effects may have a considerable influence on the success of a restoration project. Without taking certain factors into consideration, such as planting order, interspecific competition between natives and exotics, and soil nutrient levels, any restoration efforts may quickly fail. Typically, exotic species have an advantage in colonizing a recently disturbed ecosystem due to their inherent plant traits such as seed dispersal, rapid growth rate, and competitive ability over native species (Hess 2019). These advantages come in the form of resource sequestration (the reduction of available resources such as light, soil nutrients, and water in an ecosystem) (Young et al. 2001, Fukami 2015), alteration of soil microorganism and mycorrhizae (Kourtev et al. 2002), and the use of allelopathic effects, which have the ability to alter the soil chemistry, preventing growth by natives, and promoting the colonization of the exotic species (Mangla and Calloway 2008). The focus of restoration ecology is to promote the growth of native species, while preventing the invasion and establishment of exotic species (Hess 2019).

There are at least two ways this goal can be approached. The first is managing the priority effects of exotic species through removal and maintenance of the plant community. Many studies have shown exotic plants' ability to elicit strong priority effects in an ecosystem (Dickson et al. 2012, Cleland et al. 2015, Wilsey et al. 2015, Stuble and Souza 2016), easily outcompeting native species by their ability to remain after removal through soil legacies (soil modifications created by a species of plant, such as dormant seed banks, that allow them to remain in an ecosystem after removal or death (Hess 2019)), ability to establish earlier in the growing season (Dyer and Rice 1997, Seabloom et al. 2003, Munter 2008, Wolkovich and Cleland 2011) and allelopathy (where a plant releases chemicals, called allelochemicals, into the soil through process of decomposition and leaching, which can either inhibit or promote the growth of plants in an ecosystem (Ismail 2017, Rice 1984)).

The second method is to plant species of native plants that can exert stronger priority effects, thus outcompeting the exotic species and preventing substantial invasion. We can promote the strength of native species' priority effects by planting them well in advance of any invasion by exotic species, giving the native plants time to establish themselves in the community. Using plants in which their niche in the environment overlaps with that of invading exotic species and manipulating characteristics of the native species, such as mycorrhizae and allelopathic effects, can increase the strength of native plants' priority effects (Hess 2019). If native plant communities can arrive and establish during early successional periods, pre-empting available resources, they will be able to further strengthen their priority over exotic species that arrive later (Yu 2020, Ploughe et al. 2020). This method has a lot of potential in the world of restoration as it gives researchers the ability to be less disruptive in an environment, through the removal of and controlling the growth of exotic species and allowing naturally occurring species of plants to do the work.

Priority effects have a significant impact on community assembly, but further research is necessary to understand the impacts they have on restoration and invasion ecology (Cleland et al. 2015).

SOIL AMENDMENTS EFFECTS ON PLANT GROWTH

Soil amendments can play a role in deciding the makeup of species in an ecosystem and the overall outcome of a restoration project. There is a range of soil amendments that can be used, with different purposes and benefits for each amendment type. Chemical fertilizer is one such soil amendment, which increases nutrient availability in the soil. This type of amendment has been proven to increase the productivity of plants that grow in the early season, while being detrimental to the productivity of species that grow later (Jarchow and Liebman 2012). However, while the additional nutrients, particularly nitrogen, has proven to help with early growth, it has also been proven to promote the growth of non-native species due to their ability to sequester nutrients and take advantage of increased nutrient levels, excluding native species growth (Suding et al. 2005). Straw matting is another soil amendment, provides no significant increase to native grasses and forbs' population size yet decreasing the population size and invasion potential of non-native grasses and forbs (Huddleston 2005). Using wood ash or biochar to amend soil can help to improve soil nutrient availability and retention, increase organic matter adsorption, and soil aeration (Ohsowski 2012). Applying compost as a soil amendment can reduce bulk density, enhance filtration, and increase plant available water in the soil, as well as increase nutrient levels in runoff and reduce sediment loss (Kranz et al. 2020). Soils amended with biosolids have been found to increase essential elements, macronutrients, and micronutrients essential for plant growth, while also allowing for an eco-friendly use of biosolids. It is imperative that the correct amendment types are used, and in the end, the goal of the restoration project will determine what soil amendment will be best suited for said project (Ohsowski 2012).

For my project I tested two soil amendments: straw matting and biochar mixed with fertilizer, plus the combination of the two amendments, to determine their relative effects on native plant growth and the ability to ward off exotic species.

My project will focus on using priority effects and soil amendments to restore semi-arid grasslands, which have become increasingly disturbed due to anthropogenic disturbances and poor land management (Lal 2001). Restoration in a semi-arid setting is difficult due to a lack of various environmental factors, namely the lack of water for plant growth and ecosystem stability (Wang et al. 2008) and lack of available nutrients for plant growth (Feng et al. 2013, Ouyang et al. 2016) as well as the increased odds of invasion by exotic species in recently disturbed sites (Macdougall 2008). The ability to establish earlier in the growing season and quickly sequester available nutrients and water allows non-native exotic plants, in particular spotted knapweed (*Centaurea stoebe*), to take over recently disturbed semi-arid grasslands (Pysek and Richardson 2008, Dickson et al. 2012).

My research uses ecological theory and restoration practices to examine how planting order and priority effects impact biodiversity, plant growth, and the rate of invasion of unwanted exotic species following a simulated disturbance event. I also use an array of soil amendments to test how additional nutrients in the soil affect plant growth and arrival order. More specifically, this study explored three main research questions:

1.) How will the arrival order of native species, based on successional strategy and plant functional groups, affect the productivity and biodiversity of the native plant community, and reduce the invasion of unwanted non-natives in a recently disturbed grassland ecosystem?

2.) Do straw matting and biochar, as soil amendments, affect the productivity and biodiversity of the native plant community, and the rate of invasion in a recently disturbed grassland ecosystem?

3.) What combination of soil amendment and planting order creates the most ecologically diverse and stable native plant community while also deterring invasion by unwanted exotic species?

To answer these questions, I performed a two-part study: (1) a field study that focused on how the planting orders, in combination with soil amendments, functioned in a real-world setting, and (2) a greenhouse study conducted to test how the plants interacted with each other, and how the plants interacted in the face of invasion (spotted knapweed), in a controlled greenhouse setting. This two-part approach enabled a broad approach to examine treatment effects in the real world and allow the opportunity to observe details that play a part in determining success or failure during a grassland restoration project, post construction.

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CHAPTER 2: SOIL AMENDMENTS AND PRIORITY EFFECTS ON NATIVE PLANT GROWTH AND DETERANCE OF EXOTIC PLANT SPECIES IN A RECENTLY DISTURBED SEMI-ARID GRASSLAND

INTRODUCTION

An ecological disturbance can be described as "a cause; a physical force, agent, or process either abiotic or biotic, causing a perturbation (which includes stress) in an ecological component or system; relative to a specified reference state and system; defined by specific characteristics" (Vitousek and White 1981, Bazzaz 1983, Rykiel 1985). Plant communities are particularly at risk of disturbances such as rising atmospheric greenhouse gas concentrations, biotic invasions creating altered community assemblages, and anthropogenic land use change (Steffen et al. 2006), creating a change in habitable ranges for many species due to changes in temperatures, weather, water availability, and nutrient availability (Dawson et al. 2011), as well as shifts in ecological niches, population dynamics, and plant functionality (Franklin et al. 2016).

Grasslands are declining globally (Samson et al. 2004) and are more susceptible than other ecosystems to major worldwide disturbance and climate events, namely drought and flooding (Arnone et al. 2008, Arnone et al. 2011, Hoover 2014). While semi-arid and arid grasslands tend to be resilient, over time they will also feel the effects of long-term drought events (Evans et al. 2011). These major disturbance events have a long-term effect on community composition, causing loss of dominant species and allowing for ease of recruitment by ruderals and invasion by dominant opportunistic exotics and weedy species (Ewel 1986, Hobbs 1989, Rejmanek 1989, Hobbs 1991, Hillebrand et al. 2008, Evans et al. 2011, Lloret and Escudero 2012, Hoover 2014). The loss, or shift, of dominant species has also been shown to have long term significant effects on native ecosystem functions (Smith and Knapp 2003, Breshears et al. 2005, Sasaki and Lauenroth 2011).

There are also natural disturbance events that historically affect grasslands such as fire, grazing, and trampling (Hobbs 1992). These forms of disturbance can, at times, be beneficial to an ecosystem, by thinning out debris and allowing for native opportunistic species to claim a stake in the ecosystem (Pickett and White 1985).

Construction, heavy machinery use, and other anthropogenic induced disturbances have become increasingly more common (Vitousek et al. 1997, Kareiva et al. 2007, Ploughe and Fraser 2022) and extensively degrade ecosystems by deteriorating soil health (Soon et al. 2000, Chen and Gao 2006, Kowaljow and Rostagno 2008, Olson and Doherty 2012, Shi et al. 2014), shifting from desired to undesired ecosystem states (Sinclair et al. 2007, Sasaki et al. 2015), and lowering overall diversity of the plant communities (UN Environment Program 1995, Benitez-Malvido 2006, Fløjgaard 2022). During construction projects excavation and use of heavy machinery can increase soil erosion, while also reducing stability of the soil, and mixing soil horizons, thus altering soil characteristics (Yu et al. 2010, Desserud et al. 2010, Olson and Doherty 2012). Soils found in pipeline ROWs have been found to have lower total organic matter and higher pH levels than reference soils (Soon et al. 2000, Kowaljow and Rostagno 2008). In addition to the effects on soil, these disturbances have a direct effect on the ecosystem functions and ecological properties of an ecosystem (Millenium Ecosystem Assessment 2005), causing drastic and unpredictable shifts from a desired to an undesired ecosystem state (Sasaki et al. 2015). In this field study I will be attempting to provide context into potential methods of restoration in the interior British Columbia grasslands after a major anthropogenic disturbance event occurs.

Recent concerns over worldwide environmental changes, loss of soil organic matter, and long-term sequestration of carbon stocks in nutrient deficient soils has led to researching reliable methodologies that address these concerns while remaining economically viable and realistic for restoration managers, farmers, and others who may need to answer these problems (Lehmann et al. 2006, Lehmann 2007, Laird 2008, Jones 2011, Jones 2012). Soil organic matter loss has been linked with soil quality decline, decreased plant growth, and ecosystem service loss.

Biochar is produced through a process called pyrolysis, which is the burning of biomass (in this case trees) under temperatures ranging from 400-500 °C (Czernik and Bridgewater 2004, Lehmann 2007). Biochar has numerous noted benefits to the ecosystem. Biochar has proven to be a reliable long term carbon sequestration and storage method when incorporated into the soil while also introducing long term soil nutrients (Lal 2008, Sohi et. al. 2010). Biochar also has potential benefits pertaining to remediation by binding to organic pollutants and toxic heavy metals, while also increasing long term soil structure (Cao et al. 2009, Chen and Chen 2009). Furthermore, biochar has proven to increase soil microbial biomass and enzymatic activities (Smith et al. 2010, Jones et al. 2011, Lehmann et al. 2011), reduce N_2O emissions (Taghizadeh-Toosi, 2011), suppress and prevent plant disease in treated soils (Elad et al. 2010), and increase soil moisture and plant available water (Jeffery et al, 2011, Novak et al. 2012, Basso et al. 2013, Masiello et al. 2015, Haider et al. 2017).

Biochar also has been found to have numerous benefits on plant productivity. It has been found to cause earlier germination compared to controls due to biochars dark surface causing an increase in surface albedo, allowing for longer periods of growth (Genesio et al. 2012), larger production of biomass due to increases in soil moisture and plant available water (Kammann et al. 2011), and an increase of soil phosphorus and potassium (Biederman and Harpole 2013). In a meta-analysis conducted by Biedermand and Harpole (2013) it was found that biochar treated sites had an increase in aboveground biomass production in all plants, and an increase of belowground biomass production in only annual plants.

In contrast, biochar can have negative effects on plant growth, ecological development, and environmental impacts due to biochar having a high C:N ratio (500:1). It is possible that the high carbon ratio in biochar may lead to a nutrient tie-up in treated soils, leading to reduced plant biomass. However, with the addition of nitrogen (fertilizer and biochar mixed treatment) there is an increase in plant growth (Bista 2019, Van Swieten 2010).

Furthermore, it has been suggested that biochar can reduce soil organic matter and promote soil humus loss (Wardle et al. 2008). Biochar production can introduce atmospheric pollutants into the local ecosystem and become detrimental to human health (Kato et al. 2004, Barbosa et al. 2006). Lastly, biochar production can increase clear cutting to produce wood for the products, thus causing further soil degradation and erosion (Ayoub 1998).

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A recurring problem for disturbed sites, especially those with loss of vegetation and soil structure, is the ensuing erosion and loss of stable soil due to runoff and losing the anchoring factors of long-term root systems (Cerda 2007, Garcia-Orenes et al. 2009, Hee Won et al. 2012). In addition, grasslands in Western North America are susceptible to low soil moisture and a high variability in precipitation, making the growing season temporal and unpredictable (Knapp and Smith 2001, Bakker et al. 2003, Oliveira et al. 2013), while disturbed sites have higher amounts of exotic species due to their ability to quickly colonize deteriorated and nutrient deficient ecosystems without much native competition (DiTomaso 2000, Young and Clements 2005).

The use of straw mats has many potential benefits. It has been suggested that the use of straw mats can help decrease soil erosion, increase soil moisture, and decrease the growth of unwanted weedy species (Steinfeld et al. 2007, Hee Won et al. 2012). Mats using thermoplastic non-biodegradable polymer netting can introduce a multitude of environmental problems, such as soil pollution and the introduction of micro plastics into a site that is already being remediated or restored (Prambauer et al. 2019, Wu et al. 2020). However, there are numerous biodegradable alternatives present in the market that provide similar benefits compared to the non-biodegradable mats (Prambauer et al. 2019). Furthermore, straw mats can reduce the growth of all plants. While this is beneficial in reducing unwanted species, it is non-targeted and will reduce the growth of native species as well (Steinfeld et al. 2007). Seahra et al. (2019) used straw matting in their study, it was not a unique treatment because it applied to all plots, but they were unable to evaluate the impact of straw matting on invasion control and assist in native establishment during ecological restoration. In my study I will attempt to provide context into the benefits of straw matting in ecological restoration.

The flora configuration of a new site develops due to seed dispersal, biotic interactions, and the conditions of the surrounding environment. It has also been shown that factors such as the order of community assembly, plant arrival, and priority effects can have a strong effect on the makeup of vegetation at a newly disturbed site (Drake 1991, Weiher and Keddy 1995, Chase 2003, Ejrnaes et al. 2006). In the world of restoration and invasion ecology there is no consensus on how priority effects occur, how they interact with the surrounding environment in the field, or the potential benefits priority effects may have in reclaiming and restoring a disturbed site by pushing the site towards a target ecosystem (Fukami et al. 2005, Vannette and Fukami 2014, Cleland et al. 2015).

Few studies examined how priority effects and community assembly are affected in the face of competition between native and exotic plants (Seabloom et al. 2003, Abraham et al. 2009, Grman and Suding 2010, Stevens and Fehmi 2011, Ploughe et al. 2020). It has been suggested that exotics have strong, sometimes overwhelming, priority effects due to fast growth, high fecundity, and nutrient sequestration abilities (Pysek and Richardson 2008, Dickson et al. 2012). This allows exotics to sprout earlier, grow quicker, and create monocultures, thus significantly lowering the site diversity after disturbance (Dickson et al. 2012). However, it has been shown that when natives species are able to establish themselves in the field well before invasion, allowing the native plants to sequester nutrients and space, there is an increase in species diversity and a decrease in total exotic populations (Mwangi et al. 2007, Dickson et al. 2012, Yu et al. 2020). This is important because creating a diverse native plant community will allow for higher utilization of soil nutrients (Dimitrakopoulos and Schmid 2004, Scherer-Lorenzen et al. 2003) and limit resources available for any colonization by exotic species (Hector et al. 2001, Fargione et al. 2003). It has been suggested that exotic forbs and annual grasses germinate more quickly in some settings, including in response to the rainy season in semi-arid grasslands, allowing them to emit stronger priority effects (Wainwright et al. 2012).

It is well known that early successional plants tend to be able to emit stronger priority effects in a newly colonized ecosystem (Erikkson and Erikkson 1998, Sarneel 2016, Yu et al. 2020, Ploughe et al. 2020), but the benefits of establishing late successional grasses and forbs prior to the arrival early successional grasses and forbs has not been well studied. Middleton and Bever (2012) showed that using a soil inoculation from an already established late successional grassland community positively affects the growth and establishment of late successional species, while being detrimental to the establishment of early successional species. In my study I will manipulate the order of arrival between early and late successional plants and examine how priority effects change with differing seeding orders and usage of different amendments.

Objectives

1) Test native plant species' priority effects, and if they can help deter invasion by exotic species.

2) Examine the effects of different seeding orders of native successional plants on average growth across native species.

3) Evaluate what combination of seeding order and amendment application promotes the greatest average growth of native species while deterring invasion of exotic species.

4) Examine what soil amendments promote the most growth in native plants while also deterring invasion by exotic species.

Predictions

I hypothesize that if the early successional native grasses and forbs are planted at the same time as the late successional native grasses and forbs there will be a higher amount of productivity and diversity (in terms of richness and evenness), and a lower rate of cover of exotic species across all amendment types. Planting all successional species during the second seeding of the field trial, after a cover crop during the first seeding, will yield the lowest overall productivity and diversity across native species and have the highest amount of exotic invasion. This will be due to the cover crop and potential invaders being able to sequester the nutrients prior to the arrival of the native successional species, leaving low amounts of nutrients available in the soil for the successional species to establish.

Additionally, I hypothesize that biochar with straw matting will allow for the most productivity and diversity when early successional species are seeded prior, or at the same time (during the first planting of the field trials) as late successional native species. Early successional species' ability to sequester the continuous release of nutrients from the biochar providing nutrients to the late successional species will allow for even growth. All other seeding orders that are treated with a biochar will experience a greater amount of growth and diversity over other amendment types.

When examining how the amendments will affect invasion and growth of unplanted and volunteer species, I predict that the greatest amount of invasion will be in the control plots that experience no amendment. The plots that have straw matting as an amendment will experience the least amount of invasion and growth of species not planted. I expect this to be due to the straw matting's ability to deter the germination of seeds arriving after its placement, blocking those seeds to find their way to the soil underneath, thus preventing their ability to establish themselves.

Lastly, I hypothesize that there will be a greater water content in the plots that receive the two amendment types, and plots that receive the biochar treatment will have a higher amount of water content in the soil. In terms of organic matter (OM) content present in the soil, I think there will be a similar trend to water content where the sites that receive the soil amendments will have a higher OM. When looking at pH levels, available nitrogen, available phosphorus, and available potassium in the soil, I think there will be no notable change in plots that only receive the straw matting treatment. In contrast, plots that receive the biochar and fertilizer treatment will have a lower pH level and higher amounts of available nitrogen, phosphorus, and potassium (Biederman and Harpole 2013, Zhang 2019).

METHODS

Site Description

The field study was conducted at three sites located in Kenna Cartwright Nature Park in Kamloops, British Columbia. The study sites are in the Ponderosa Pine PPxh2 Biogeoclimatic Zone and Bunchgrass Zone BGxw1 (Government of British Columbia Ministry of Forestry 2018).

Characterized as very dry and hot, the Ponderosa Pine Zone is the warmest and driest forest zone in British Columbia. The zone experiences an average annual temperature of 7.27℃ to 8.63℃ and average annual precipitation of 273.5 mm to 322.83 mm. The Ponderosa Pine zone is dominated by open savannah-like stands of Ponderosa Pine with an understory abundant with grasses that experience frequent ground fires. However, the period of the year that I am most concerned about for this study is the growing season which lasts 5 to 6 months. The days during the growing season are long and hot, with cool nights and a mean warmest month temperature of 19.5℃ to 20.97℃ and a mean growing season (May to September) precipitation of 96 mm to 127.3 mm (Hope, Lloyd, Mitchell et al. 1991, BC Climate Explorer 2021).

The Bunchgrass Zone occurs at a lower altitude compared to the Ponderosa Pine Zone, characterized by warm to hot, dry summers and moderately cold winters with low snowfall. The zone experiences an average annual temperature of 6.48℃ to 7.05℃ and average annual precipitation of 311.67 mm to 344 mm. The Bunchgrass zone is dominated by shrubs, and bunchgrasses. During the growing season, the mean warmest month temperature of 18.23℃ to 19.41℃ and a mean growing season (May to September) precipitation of 121.17 mm to 166.67 mm (Nicholson, Hamilton, Harper, Wikeem 1991, BC Climate Explorer 2021).

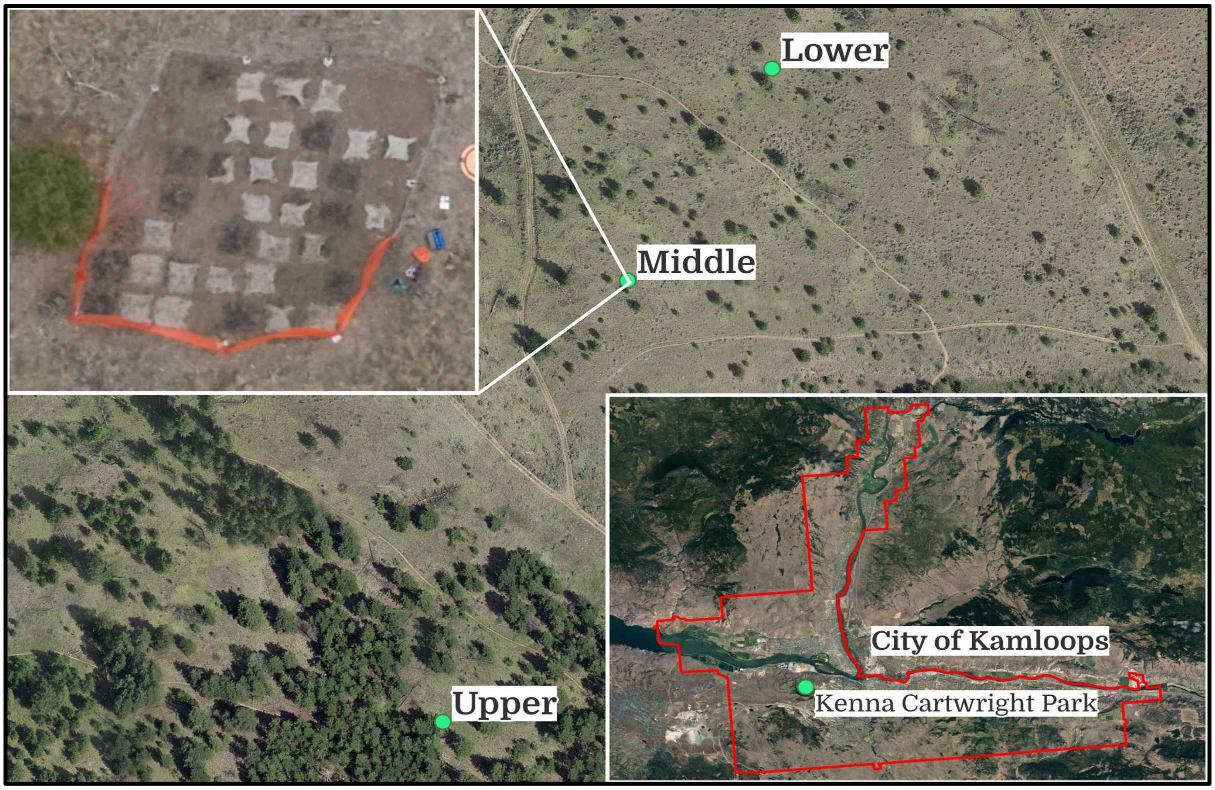

Figure 2.1: Location of sites in Kenna Cartwright Park. Each site located within a different BEC zone (Upper = Ponderosa Pine; Middle = Transition between Ponderosa Pine and Bunchgrass; Bottom = Bunchgrass)

Three study sites (Figure 2.1) were established within Kenna Cartwright Park varying in altitude and Biogeoclimatic Zones. Site 1, the site highest in altitude, was located at 50°40'28.5"N 120°23'49.0"W within the Ponderosa Pine PPxh2 Biogeoclimatic Zone. The size of site 1 was 13 meters by 5 meters. Site 2 was located at 50°40'35.0"N 120°23'45.2"W along the transition between the Ponderosa Pine PPxh2 and Bunchgrass BGxw1 Biogeoclimatic Zones. The size of site 2 was 8 meters by 8 meters. Site 3, the site lowest in altitude, was located at 50°40'35.0"N 120°23'41.0"W within the Bunchgrass BGxw1 Biogeoclimatic Zone. The size of site 3 was 8 meters by 8 meters.

Study Design

Prior to seeding, a few preliminary tests were conducted. A germination test (Appendix A) on all seeds procured was conducted to test the percentage germination. This was done by using a petri dish and placing filter paper (Whatman 4 filter paper, 20-25 μm pore size) in the dish. Then 20 seeds of the same species were placed in the petri dish, placed in a greenhouse, and kept moist over a period of 3 weeks. To be considered "germinated" the seed had to have a visible root or stem shoot extending from the seed. This was replicated in groups of four for each species. This allowed me to test which procured seeds had the highest germination rates. The results of the test (Appendix A) were used for both the field trials in Kenna Cartwright Park (Chapter 2) and in the greenhouse trials (Chapter 3).

The seeding density of each species used in the seed mixes was calculated using average weight in tandem with the germination results (Appendix A). To do this the weight of 100 seeds for each species was taken three times. Then the average of those three weights was used when weighing out the seeds for the seed mixes. The average weights of the seeds used are shown in Appendix A. A total seed density of 800 seeds at each plot was used. This means each seed mix was to have 100 viable seeds of each species. Viable seeds were calculated using the germination percentages in the germination trial to figure out how many seeds would be needed to have 100 viable seeds. Using the average weight per 100 seeds, I calculated the necessary weight for each species of seed for each seed pack. These weights for each species were then used to make the seed packs used in the field.

Before the first seeding occurred, the study sites were established in Kenna Cartwright Park. Exclosures were set up around each of the three sites using orange ski fence and chicken wire to ward off and deter animals in the park. Each site was then cleared of all vegetation and tilled to remove all vegetation. Once each site was tilled and cleared, using a 1 meter by 1 meter plot, the soil amendments were placed in accordance with the maps shown in Figure 2.2. The placement of the soil amendments was randomized. If a plot was to receive the 50:50 compost (Figure 2.2) and biochar (Figure 2.3) mixture, then an even mix of one kilogram of compost and one kilogram of biochar was mixed into the top 5cms of the 1 meter by 1 meter plot. The initial seeding treatment that was received was then sown on the plot, mixed in with the soil, and watered to help the seeds settle into the soil. If a plot was to receive straw matting, then a 1 meter by 1 meter piece of straw matting was placed over top of the whole plot and secured using four sod nails at each corner of the matting.

Total Nitrogen (N)	0.5%
Available Phosphate (P_2O_5)	0.5%
Soluble Potash (K_2O)	0.5%

Figure 2.2: Nutrients breakdown of the CIL © Composted Manure used in the field study.

Fixed Carbon	>85%
Ash	<10%
pH	9.4

Figure 2.3: Nutrients breakdown of the BC Biochar © 2-6mm Blackbear Biochar used in the field study.

Site 1

SA4	SA4	SA4	SA2	SA3	SA4	SA1	SA3	SA4	SA4	SA1	SA4
SA3	SA4	SA1	SA4	SA2	SA1	SA2	SA1	SA3	SA1	SA4	SA3
SA3	SA1	SA3	SA3	SA4	SA2	SA4	SA2	SA1	SA2	SA3	SA1
SA1	SA3	SA2	SA1	SA2	SA2	SA2	SA2	SA2	SA3	SA2	SA3

Site 2 and 3

SA1	SA2	SA4	SA2	SA4	SA3	SA3
SA3	SA1	SA2	SA2	SA4	SA4	SA1
SA4	SA3	SA1	SA2	SA4	SA1	SA3
SA4	SA1	SA2	SA3	SA2	SA4	SA3
SA1	SA4	SA3	SA1	SA3	SA2	SA4
SA4	SA3	SA1	SA3	SA4	SA1	SA2
SA1	SA3	SA2	SA1	SA2	SA2	

= Straw Matting

= Straw Matting + Biochar-Compost Mix

= Biochar-Compost Mix

= Control

SA1 = Annual Ryegrass Cover Crop First
SA2 = Early Successional First
SA3 = Late Successional First
SA4 = Early and Late Together first

Figure 2.4: Representation of the randomized experimental treatment layouts for the sites.

There were three treatment sites within Kenna Cartwright Nature Park, with each site consisting of a 4x4 factorial design (four amendments and four seeding orders) for a total of sixteen unique treatment types. Each treatment was replicated three times at each treatment site for a total of 48 plots. Each plot measured 1 meter by 1 meter (Figure 2.4).

The four amendment types that were used in this study were a 1) control group receiving no soil amendment, 2) straw matting, 3) a 50:50 biochar and compost mix (2 kilograms total), and 4) receiving both straw matting and the 50:50 biochar and compost mix (Table 2.1).

Table 2.1: A list of all 16 treatment plans that can occur on a field plot, including year 1 and 2 seeding treatments and soil amendments.

#	Year 1 Seeding Treatment	Year 2 Seeding Treatment	Soil Amendment
1	Cover Crop	Mix of 4 Early and 4 Late Successional	Control
2	Cover Crop	Mix of 4 Early and 4 Late Successional	Straw Matting
3	Cover Crop	Mix of 4 Early and 4 Late Successional	50:50 Mix of Compost and Biochar
4	Cover Crop	Mix of 4 Early and 4 Late Successional	Straw Matting + Compost and Biochar mix
5	4 Early Successional	4 Late Successional	Control
6	4 Early Successional	4 Late Successional	Straw Matting
7	4 Early Successional	4 Late Successional	50:50 Mix of Compost and Biochar
8	4 Early Successional	4 Late Successional	Straw Matting + Compost and Biochar mix
9	4 Late Successional	4 Early Successional	Control
10	4 Late Successional	4 Early Successional	Straw Matting
11	4 Late Successional	4 Early Successional	50:50 Mix of Compost and Biochar
12	4 Late Successional	4 Early Successional	Straw Matting + Compost and Biochar mix
13	Mix of 4 Early and 4 Late Successional	N/A	Control
14	Mix of 4 Early and 4 Late Successional	N/A	Straw Matting
15	Mix of 4 Early and 4 Late Successional	N/A	50:50 Mix of Compost and Biochar
16	Mix of 4 Early and 4 Late Successional	N/A	Straw Matting +Compost and Biochar mix

In addition to the four amendment types, there were four seeding treatments to test arrival order on priority effects. The first seeding order consisted of an annual agronomic grass, Italian annual ryegrass (*Lolium mutliflorum*) as a cover crop planted in May of 2021, with a mix of all eight native species (five grasses and three forbs, with at least one of each group being either an early arriving species or a late arriving species) planted in September of 2021 after the growing season.

The second seeding order consisted of four early arriving native species (two grasses and two forbs) planted in May of 2021, and four late arriving native species (three grasses and one forb) planted during September of 2022 after the growing season.

The third seeding order was the same as the second seeding order, but the ordering of the two planting groups was flipped. In May of 2021, a seed mix consisting of four late arriving native species (three grasses and one forb) was planted, then a seed mix consisting of four early arriving species (two grasses and two forbs) was planted after the growing season in September of 2021.

The final seeding order tested was the planting of eight native grasses and forb species (five grasses and three forbs, with at least one of each group being either an early arriving species or a late arriving species) during the spring of 2021 (Table 2.2).

Table 2.2. List of native forbs and grasses used in the Kenna Cartwright field trials. Plants numbered 1-4 were used in the early arrival seed mix while the plants numbered 5-8 were used in the late arrival seed mix.

#	**Common Name**	**Scientific Name**	**Type**	**Succession**
1	Blanketflower	*Gaillardia pulchella*	Native Forb	Early
2	Sandberg Bluegrass	*Poa secunda*	Native Grass	Early
3	Western Yarrow	*Achillea millefolium*	Native Forb	Early
4	Slender Wheatgrass	*Elymus trachycaulus*	Native Grass	Early
5	Rough Fescue	*Festuca campestris*	Native Grass	Late
6	Arrowleaf Balsamroot	*Balsamorhiza sagittata*	Native Forb	Late
7	Rocky Mtn. Fescue	*Festuca saximontana*	Native Grass	Late
8	Idaho Fescue	*Festuca idahoensis*	Native Grass	Late

Gaillardia pulchella (blanketflower) is an early germinating and establishing native forb (Mueggler and Stewart 1980, Tyrer et al. 2007), which has been found to compete with spotted knapweed and significantly lowers the biomass production of spotted knapweed (Callaway et al. 2004). Plant communities abundant in *Gaillardia aristata* have been found to have a higher resistance to weedy invasion due to their ability to capture soil moisture and sequester nutrients during its early growth period (Pokorny 2005, Maron and Marler 2007).

Poa secunda (Sandberg's bluegrass) is an early seral native bunchgrass (Eckert and Spencer 1986, Bernards and Morris 2016) that will grow quickly and establish after a disturbance event occurs but takes up a small portion of total vegetation due to its small growth and stature (Davies et al. 2007, Bates et al. 2009). *Poa secunda* grows early in the season before becoming dormant during the summer, and the USDA suggests it can be used early in growing seasons to compete with natives due to its quick growth (Eckert and Spencer 1986, USDA 2011).

Achillea millefolium (western yarrow) is classified as an early successional species and early seral facultative forb (USDA 2006, Nelle et al. 2000) that will heavily cover sites during the early season and early seral stage environments (Uresk et al. 2018, Curan et al. 2022).

Elymus trachycaulus (slender wheatgrass) is characterized as an early seral plant (Tilley 2011, Tilley et al. 2022) and can be a competitive grower after a disturbance event, quickly colonizing a site post-disturbance (Bartos and Mueggler 1982, Tilley 2011). *Elymus trachycaulus* has also been used as a nurse plant in some restoration cases (Ogle et al. 2014, Tilley et al. 2022).

Festuca campestris (rough fescue) is a disturbance-sensitive late successional perennial grass species (Elsinger et al. 2022) that can easily be outcompeted by and replaced by spotted knapweed (Dee et al. 1966, Lacey et al. 1989).

Balsamorhiza sagittata (arrowleaf balsamroot) is classified as a mid to late seral species in grassland and shrubland ecosystems and has difficulty colonizing recently disturbed environments (Gucker and Shaw 2018). It is a typical indicator species of climax or near-climax grasslands and shrublands (Tisdale 1947, Rumsey 1971, Franklin and Dyrness 1973). *Balsamorhiza sagittata* has been noted as economically valuable for rehabilitation of oil-shale and coal mined sites, as well as providing soil stabilization due to its long taproot (Wasser 1982).

Festuca saximontana (Rocky Mountain fescue), which is also commonly mistaken as sheep fescue (*Festuca ovina*), has been found to be a late colonizer and successor in grasslands and heathlands (Degn 2001). It can be used to outcompete weedy and exotic species in late-stage grasslands (USDA 2010).

Festuca idahoensis (Idaho fescue) has been found to be characteristic of late seral grasslands, dominating the canopy cover (Uresk et al. 2018).

First seeding took place in May of 2021 and was done in tandem with placing amendments on the plots. The procedure of seeding was done as follows: if a plot received the 50:50 biochar and compost mix it was placed down and spread evenly across the plot prior to any other amendments or seeds being placed down. Then the seed mix that the plot received was seeded. This was done by mixing the seed mix in with sand to help weigh down the seeds and stick to the soil. Then the seeds were mixed in by hand with the biochar and top part of the soil. Finally, the plot was watered to further help the seeds stick to the soil and not be blown away. If the plot received a straw matting cover, then the straw matting was placed on top of the plot and secured using sod nails at the corners of the 1 meter by 1 meter square.

Drone Multispectral Remote Sensing Protocol

A DJI Phantom 4 multispectral drone was used for aerial flights at the field plots in Kenna Cartwright Park. Flights were conducted at the beginning and end of the growing season in 2021 and the end of the growing season in 2022 for a total of three flights. The DJI Phantom 4 is a high precision quadcopter that was paired with a high precision Global Navigation Satellite System (GNSS) receiver. The multispectral camera consists of six separate sensors, including one RGB sensor for visible light and 5 monochrome sensors for multispectral imaging. The five monochrome sensors detect five separate bands, including: red, green, blue, near red, and near infrared (NIR). The multispectral camera has a Ground Sample Distance (GSD) of 18.9 cm per pixel.

These images are used to calculate the values for five different indices. The indices are normalized difference vegetation index (NDVI), green normalized difference vegetation index (GNDVI), normalized difference red edge index (NDRE), leaf chlorophyll index (LCI), and optimized soil adjusted vegetation index (OSAVI). NDVI is the measure of greenness and productivity and can be used to view growth and coverage of vegetation (Running 1990, Myneni 1995). GNDVI is like NDVI, but it uses the green bands rather than the red bands of NDVI. This measurement can show if vegetation is lacking water or nutrients (Gitelson et al. 1995). NDRE uses the red edge band between visible red light and the near-infrared spectrum. Using this band can help view the chlorophyll and sugar content of vegetation (Maccioni 2001). LCI allows the evaluation of vegetation growth and plant stress, such as nutrient stress, disease, growth, and aging (Botha et al. 2007, Houborg et al. 2009). OSAVI is based on NDVI but removes soil conditions' impact on vegetation (Huete 1988, Steven and Jaggard 1995, Steven 1998).

All measurements were taken at each of the three sites on clear days with each site being flown over on the same day. Prior to flying, and immediately after, the multispectral drone was calibrated using a white reflectance panel. This was done to calibrate the absolute reflectance and provide more accurate and reliable data. In addition to image calibration prior to flying, the drone was also connected to the GNSS to allow for accurate geo-records of all images taken during the flight. The drone was flown at a height between 30 to 50 meters above the sites, allowing for high resolution imagery to be produced.

Plant Sampling Protocol

Throughout all the vegetation surveys I did not come across or count a *Balsamorhiza sagittata* (arrowleaf balsamroot) plant, and for this reason it was not included in any of the results.

The three fescue varieties of Rocky Mountain Fescue, Idaho fescue, and rough fescue were grouped together into one group which was referred to as "fescue Spp." This was due to lack of development, making it difficult to identify individual species.

Before the second seeding that was conducted in September 2021, I conducted an initial vegetation survey of each plot at each of the three field sites. This was done by categorizing each unique plant, amendment, and bare ground, and then assigning a percent coverage of the canopy at each plot. This was done again after the second growing season at the end of July 2022.

After the second growing season the above ground biomass was collected from the center of the plot with a 0.25 meter by 0.25-meter plot. This was done by cutting the plants at soil level, then drying the plants before being weighed.

Soil Sampling Protocol

Initial soil cores were collected at each plot prior to mechanical disturbance and seeding of seeds. This was done by taking 9 cores (5 cm in height by 5 cm in diameter) at the corners of each plot, the middle of each side of each plot, and the direct middle of each plot. The cores were then combined and frozen in a freezer to be used for analysis of soil moisture content, soil pH, organic content, mineral analysis, and seed bank analysis.

Initial soil core samples were used to run seed bank analyses in the TRU research greenhouse for each of the three study sites. The study was run over a three month period and during that time only two plants sprouted, however the individuals senesced prior to being identifiable.

After the second growing season, at the end of July 2022, soil core samples were taken for each plot at each of the 3 sites. This was done by taking soil core samples (5 cm in height by 5 cm in diameter) from the center of each plot for a total of 144 samples. Before the core samples were taken, if present, the straw matting netting was cut. The soil core samples were then frozen to be used to test how the soil amendments affected the pH, soil moisture content, organic content, and mineral analysis.

Soil pH was analyzed using non-sieved samples from each of the plots. To prepare the samples, 5 grams of unsieved soil were mixed with 5 mL of deionized water. Next, the sample was homogenized and centrifuged for five minutes at 5000 rpm. Then, the samples were allowed to settle for 24 hours before using (pH measuring instrument) to measure the pH for all 144 samples.

Soil was prepped for analysis by sieving soils with a 2 mm fine mesh sieve and then dried in a Yamato drying oven (model DKN812) at 80°C for 12 hours to remove moisture. The samples were weighed before and after drying to calculate the percent moisture content for each sample.

Once dried, each sample was ground to a fine powder using a mortar and pestle to prepare for the furnace oven (Modine Model PDP). Once ground, 4 to 5 g of each sample was placed in small ceramic crucibles and placed in the furnace to burn at 500°C for 5 hours. They were then weighed again to calculate the percentage of organic matter for each sample.

The dried and ground soils were also analyzed for total carbon, nitrogen, hydrogen, and sulphur using a Thermo Scientific FlashSmart CHNS/CHNS elemental analyzer. Ten to fifteen mgs of soil were weighed and placed into small tin capsules and placed into the elemental analyzer wheel for analysis. The values were generated as a percent value of the total sample.

DATA ANALYSIS

Priority Effects Analysis

Priority effects were calculated using the priority strength calculation first described in Vanette and Fukami (2014) and later adjusted in Sarneel (2016). The cover metrics gathered during the last vegetation cover surveys conducted at the end of July 2022 were used to calculate the priority strength of the plants sown by the researchers. The strength of priority effects was calculated by using the natural logarithm of the ratio of species percent cover (D) of species (i) when it was seeded after species j and before species j (Equation 2.1).

Equation 2.1

$$\text{Priority strength} = \ln(d(i_{ji})/d(i_{ij}))$$

A positive priority strength value will depict facilitation and a negative value will depict inhibition. A priority strength value near zero means that there is no significant difference in total growth, whether the plant is sown first or second. This test allows us to directly quantify and compare the priority strength of species seeded when planted first or second in the field.

Three-factor analysis of variance (ANOVA) was performed for both planting groups (ES and LS) and each unique species seeded priority strength value to compare the effect of the four amendment treatments, the four seeding treatments, and the three unique planting sites. Site was treated as a fixed factor throughout analysis to compare the effects of site on amendment and seeding order indices.

Flora Diversity Analysis

Plant cover data from each site was compared using Shannon diversity indices, as well as species richness. In addition, a three-way ANOVA was performed for exotic coverage at each plot to compare the effect of the four amendment treatments, the four seeding treatments, and the three unique planting sites. Exotic species were identified using the invasive species list published by the Invasive Species Council of British Columbia (Invasive Species Council of British Columbia, 2022).

Site was used as a fixed factor in all statistical calculations to account for the different biogeoclimatic zones that each of the three sites were found in and to see the effect this had on other parameters measured.

Lastly, non-metric multidimensional scaling (NMDS) was used to look at the similarity and dissimilarity of species composition between plant communities in the different sites, the amendment treatment received, and the seeding treatment received. A NMDS was also run for each plot, separated by site, to look at vegetation similarity for each amendment and seeding treatment.

Soil Analysis

A three-way ANOVA was performed for soil organic matter, soil moisture, each individual soil element (carbon, nitrogen, hydrogen, and sulphur), and soil pH to compare the effect of the four amendment treatments, the four seeding treatments, and the three unique planting sites.

Multispectral Imagery Analysis

PIX4Dmapper (version 4.8.0) was used to produce the multispectral imagery captured in the field.

Orthomosaic imagery, in QGIS (version 3.26), was used as a canvas to create 1 meter by 1-meter squares placed over each individual plots (144 total over 3 sites), used to extract the spectral index values (NDVI, GNDVI, LCI, NDRE, OSAVI) for spatial analysis in R using the "sf" and "terra" packages (Pebesma 2018, Hijmans 2022). The 1 meter by 1-meter squares were attributed in QGIS to represent their assigned seeding treatment and amendment treatment.

The spectral index values were used to run three-way ANOVAs against site, seeding treatment, and amendment treatment received by the plots.

All analyses were run in R, version 4.0.5. A Q-Q plot was created for each ANOVA to check for normality, and a F-test was run for each ANOVA to check for variance.

RESULTS

Priority Effects Results

The only species that showed a significant change in their priority value based on site location was blanketflower, which had a higher priority advantage at site 1 (Figure 2.5). The priority values at sites 2 and 3 were not significantly different from each other. All other species had no significant difference in priority values when compared across all 3 sites ($F_{8,120} = 2.66$, $p = 0.009$).

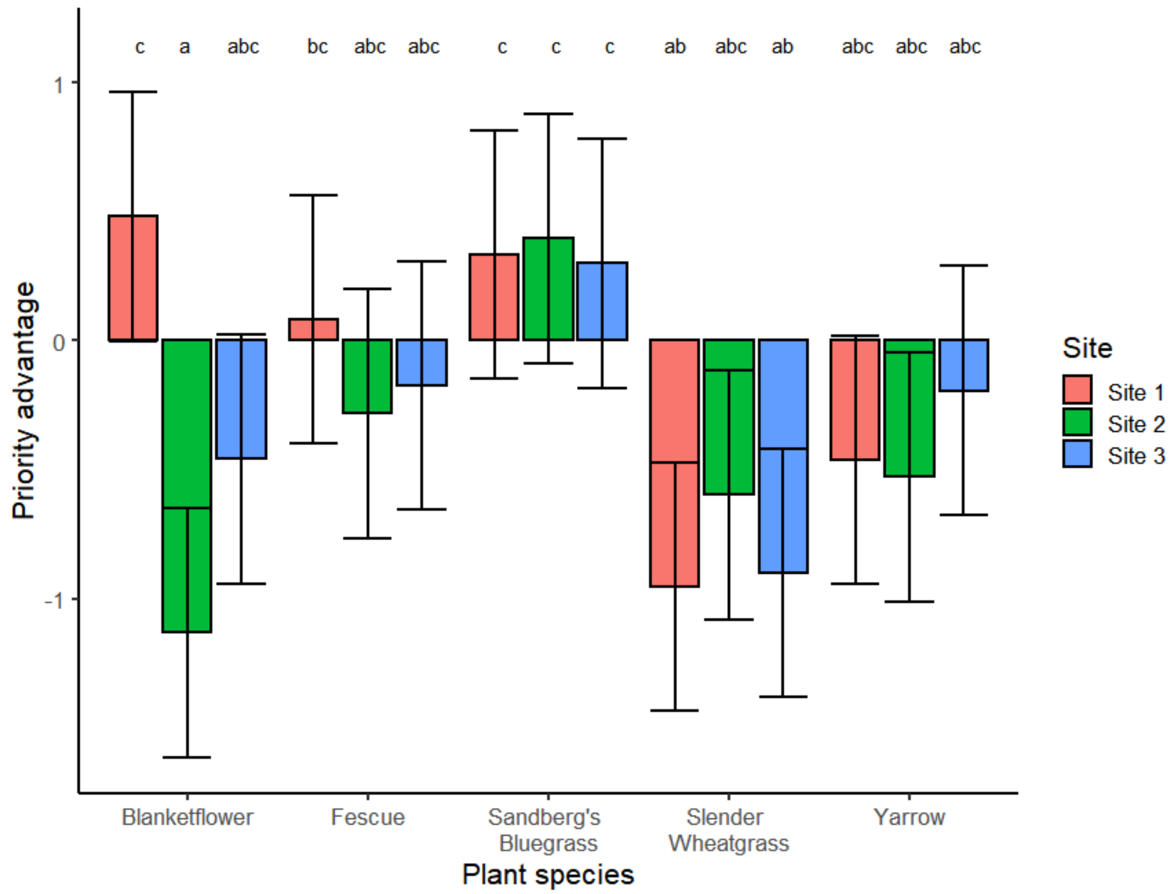

Figure 2.5: Priority advantage of each seeded plant species after 2 growing seasons post disturbance, across three research sites in Kenna Cartwright Park (± SE). A negative priority advantage indicates inhibition of growth when planted second, a positive priority advantage indicates facilitation of growth when planted second. Differences in letters above individual bars indicate significance groupings.

When total coverage of all plants seeded is taken into consideration, Site 1 had a significantly higher priority value than Site 2 (Figure 2.6). While site 3 was no different than the other two sites ($F_{2,48} = 3.652$, $p = 0.033$).

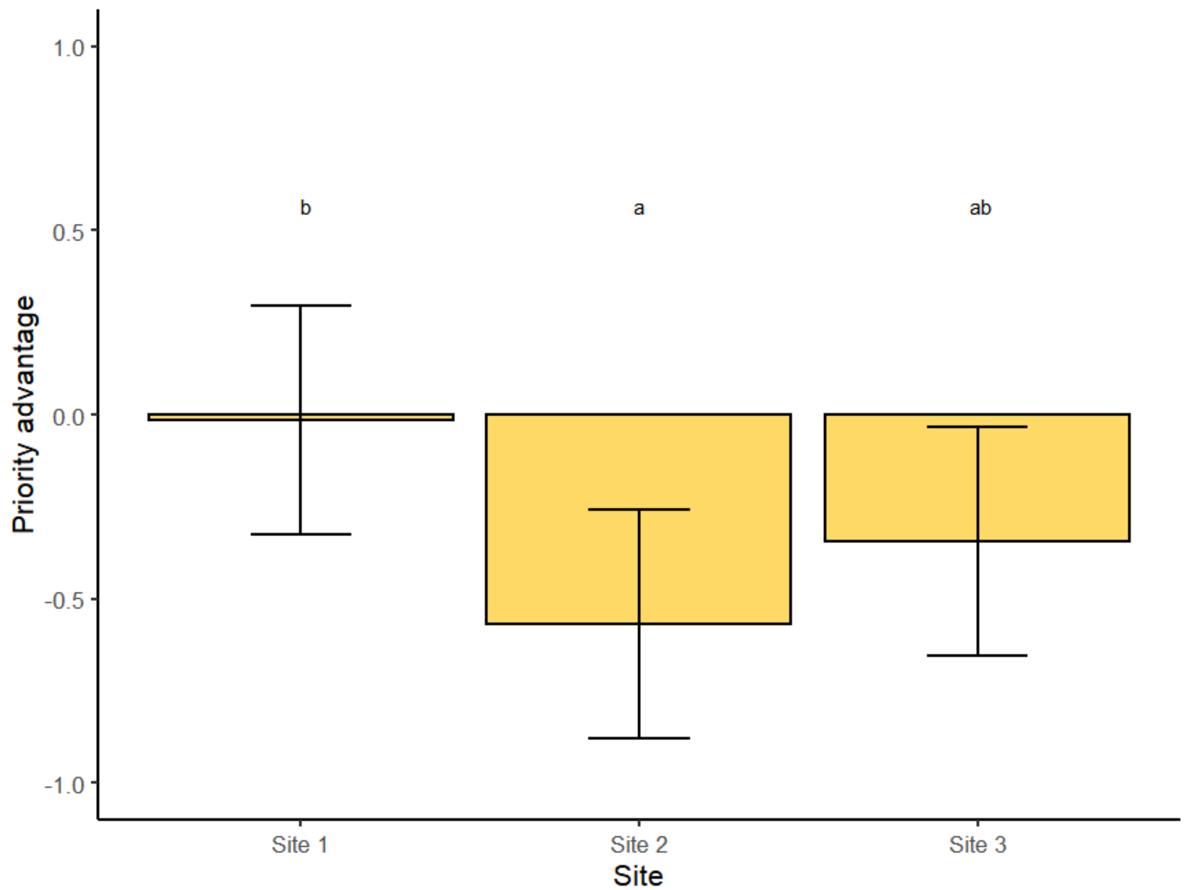

Figure 2.6: Priority advantage at each individual site after 2 growing seasons post disturbance in Kenna Cartwright Park (± SE). A negative priority advantage indicates inhibition of growth when planted second, a positive priority advantage indicates facilitation of growth when planted second. Differences in letters above individual bars indicate significance groupings.

Plants found in the ES seeding treatment had a significantly lower priority value when compared to the priority value of the plants found in the LS seeding treatment ($F_{1,48}$ = 4.763, p = 0.034) (Figure 2.7).

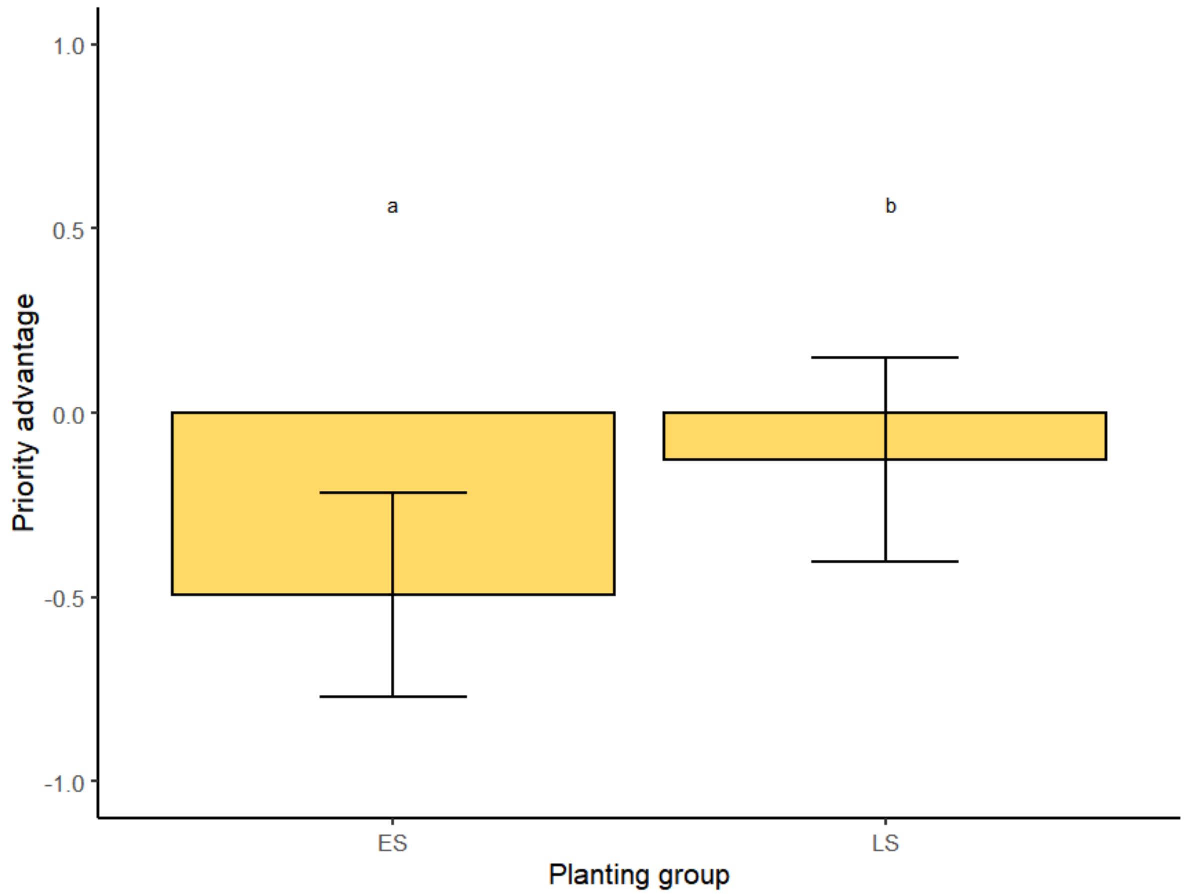

Figure 2.7: Priority advantage of planting groups after 2 growing seasons post disturbance in Kenna Cartwright Park (± SE). A negative priority advantage indicates inhibition of growth when planted second, a positive priority advantage indicates facilitation of growth when planted second. Differences in letters above individual bars indicate significance groupings.

Native and Exotic Coverage Results

Both western yarrow($F_{3,96}$=4.08, p=0.009) (Figure 2.8A) and blanket flower($F_{3,96}$=3.72, p=0.014) (Figure 2.8D) have significantly different amounts of growth depending on the amendments a plot received. Western yarrow was found to have the highest coverage in plots that received no amendment treatment, and the lowest coverage in plots that received both straw matting and biochar as amendments. Blanket flower was found to have the highest coverage in plots that received both the straw matting and biochar amendments, while the lowest coverage was seen in plots that received no amendment treatment. Slender wheatgrass ($F_{3,96}$=0.42, p=0.741) (Figure 2.8B), Sandberg's bluegrass ($F_{3,96}$=1.78, p=0.156) (Figure 2.8C), and fescue spp. ($F_{3,96}$=1.47, p=0.228) (Figure 2.8E) saw no significant difference in cover when separated by amendment treatments.

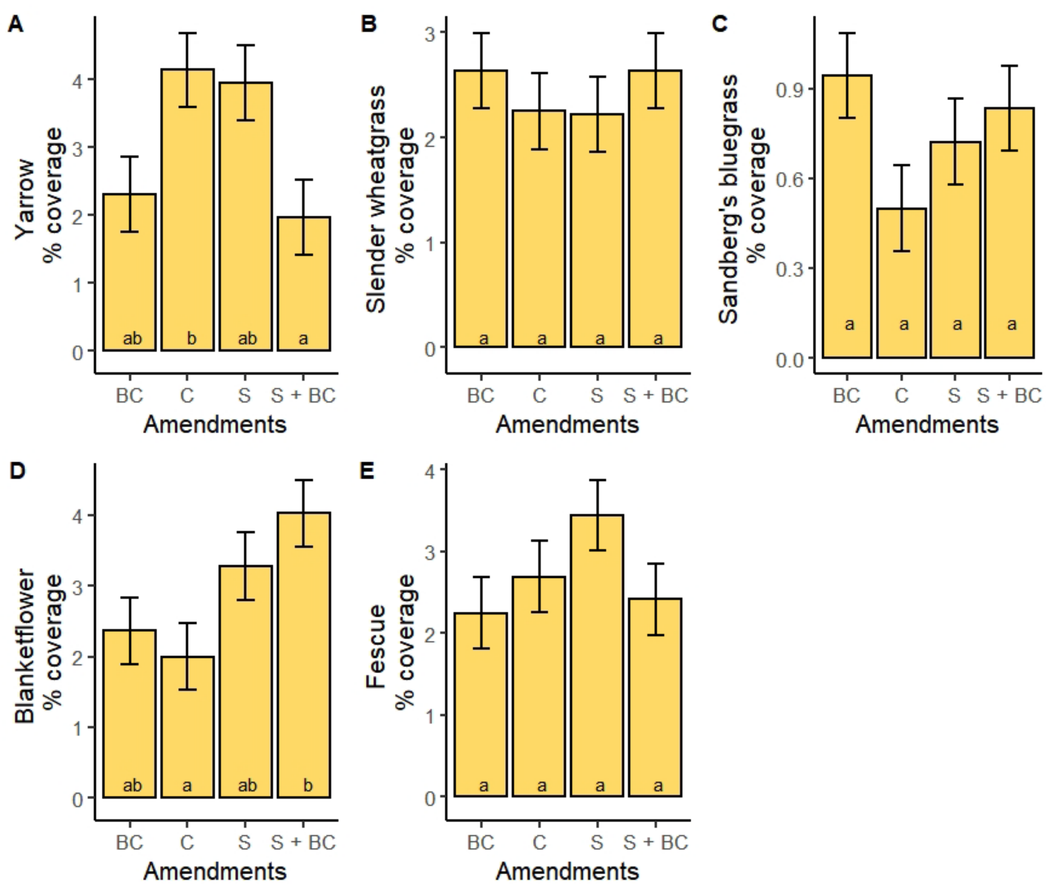

Figure 2.8: Percent of total canopy coverage of each planted species after 2 growing seasons when compared to the amendment treatment received (± SE). Differences in letters above individual bars indicate significance groupings.

When the canopy coverage of each species sown is compared to site both western yarrow ($F_{2,96}$=3.20, p=0.045) (Figure 2.9A) and fescue spp. ($F_{2,96}$=12.29, p<0.001) (Figure 2.9E) show significant results. Yarrow saw the highest total coverage at site 2 but saw the lowest coverage at site 1. Fescue spp. Saw the highest coverage at both sites 1 and 3, with a significantly lower coverage at site 2. Slender wheatgrass ($F_{2,96}$=0.97, p=0.380) (Figure 2.9B), Sandberg's bluegrass ($F_{2,96}$=2.17, p=0.119) (Figure 2.9C), and blanket flower ($F_{2,96}$=0.08, p=0.924) (Figure 2.9D) saw no significant difference in coverage based on site.

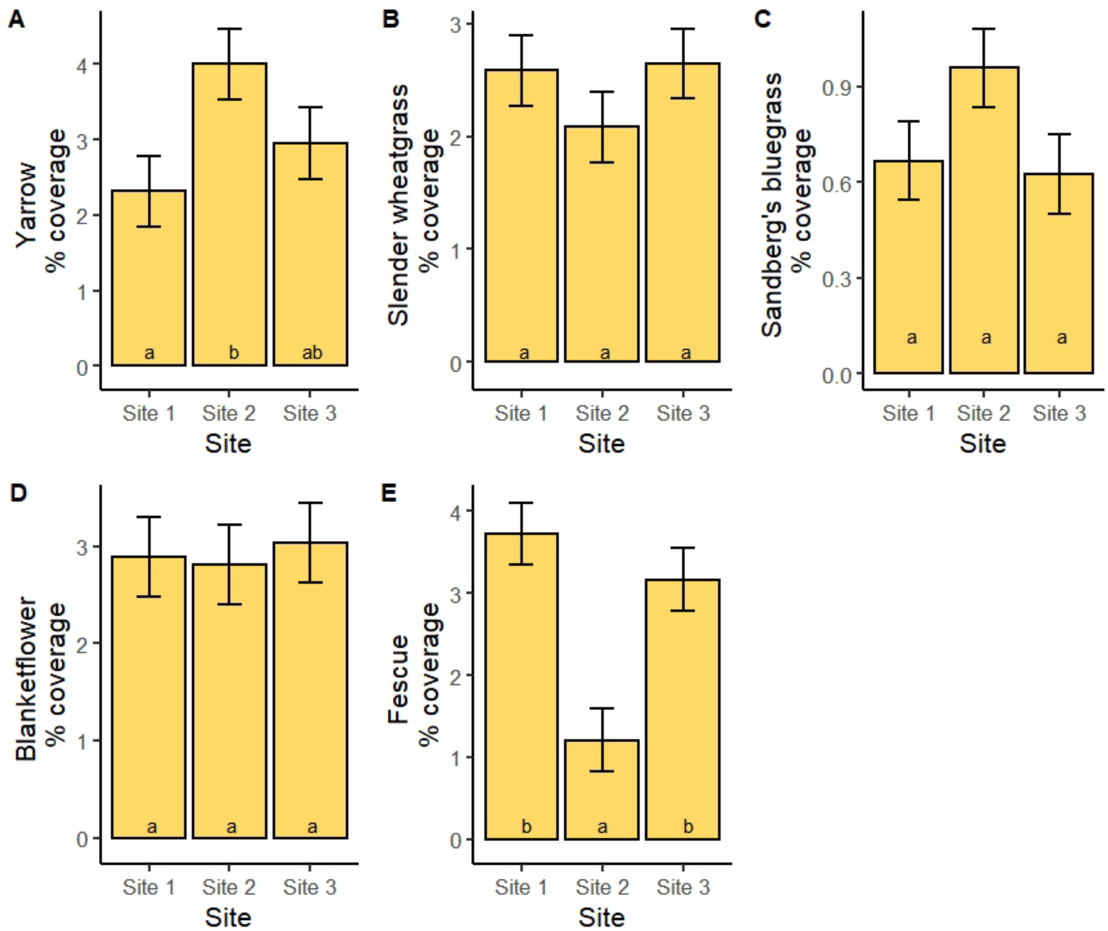

Figure 2.9: Percent of total canopy coverage of each planted species after 2 growing seasons when compared to site (± SE). Differences in letters above individual bars indicate significance groupings.

Slender wheatgrass ($F_{3,96}$=20.76, p<0.001) (Figure 2.8B), Sandberg's bluegrass ($F_{3,96}$=8.69, p<0.001) (Figure 2.10C), and blanket flower ($F_{3,96}$=6.61, p<0.001) (Figure 2.10D) saw significant difference in coverage when compared to the seeding order a plot received. Slender wheatgrass saw significantly higher coverage in plots that received the SA2 and SA4 seeding treatments but saw significantly lower coverage in plots that received the SA1 and SA3 seeding treatments. Sandberg's bluegrass saw the highest coverage in plots that received the SA3 seeding treatment and saw the lowest coverage in plots that received the SA1 treatment. Blanket flower saw the highest coverage in plots that received the SA2 and SA4 seeding treatments but saw the lowest coverage in plots that received the SA1 treatment. Both western yarrow ($F_{3,96}$=2.52, p=0.062) (Figure 2.10A)and fescue spp. ($F_{3,96}$=0.66, p=0.577) (Figure 2.10E) saw no significant response in coverage.

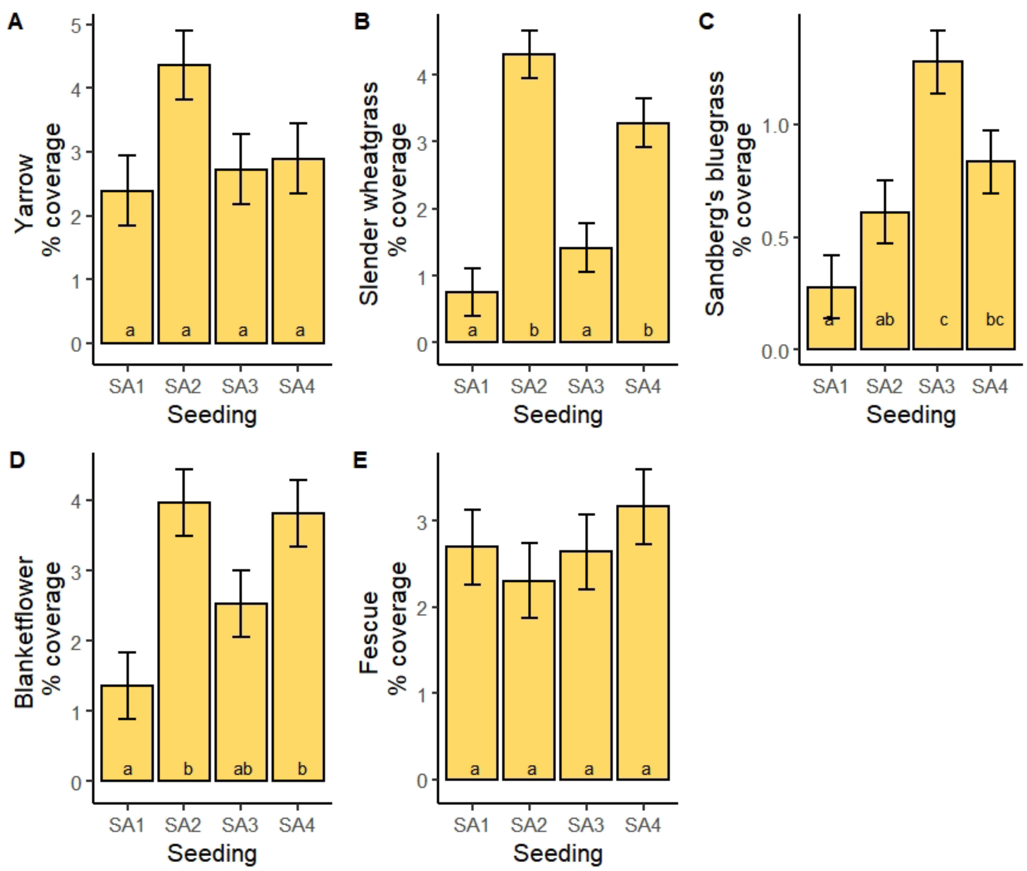

Figure 2.10: Percent of total canopy coverage of each planted species after 2 growing seasons when compared to the seeding treatment received (± SE). Differences in letters above individual bars indicate significance groupings.

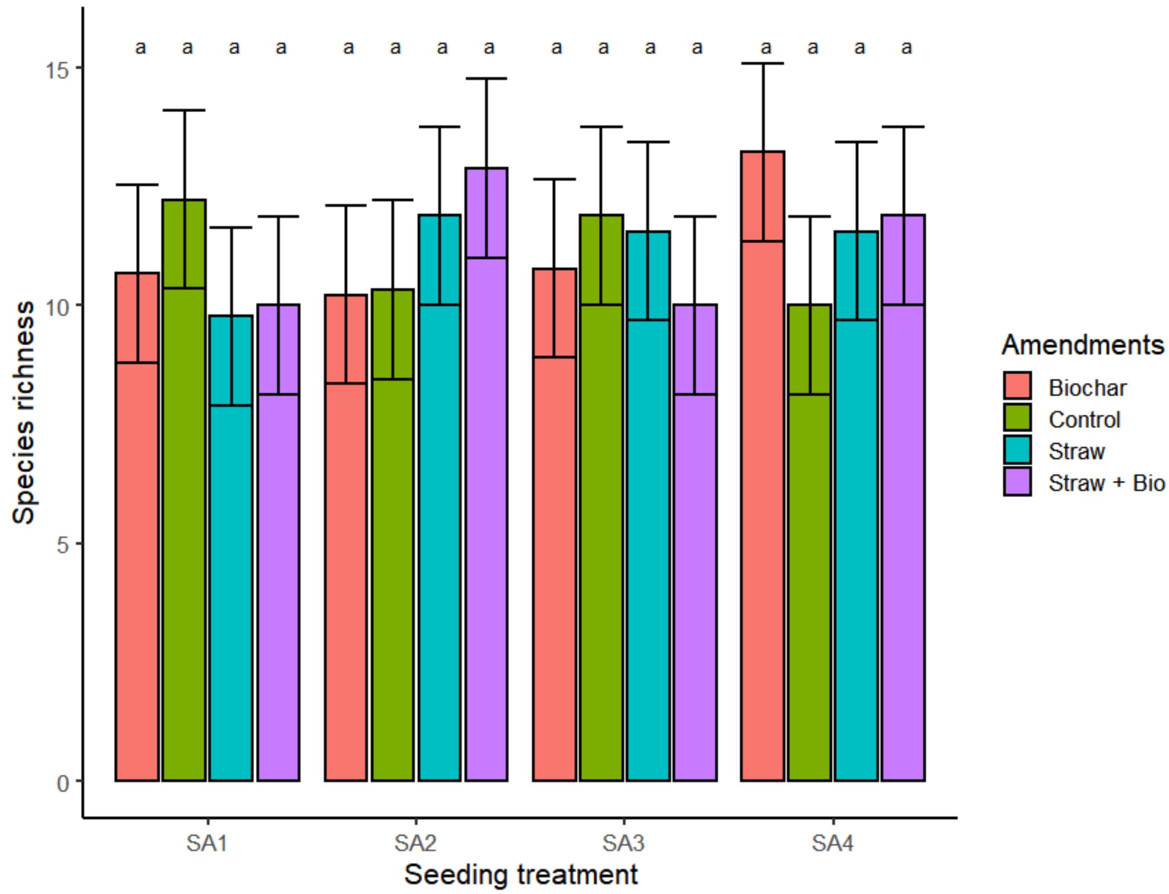

Figure 2.11: Species richness (emmean) at plots receiving the four different seeding groups when grown in different soil amendments after 2 growing seasons post disturbance in Kenna Cartwright Park (± SE). Differences in letters above individual bars indicate significance groupings. There is no significance in Shannon diversity when compared across seeding groups and soil amendment types.

The species richness was measured for each individual plot at each site, then the mean species richness was taken for each site and compared. A significantly higher species richness was observed at site 2 compared to both sites 1 and 3 ($F_{2,94} = 7.336$, $p = 0.001$) (Figure 2.12).

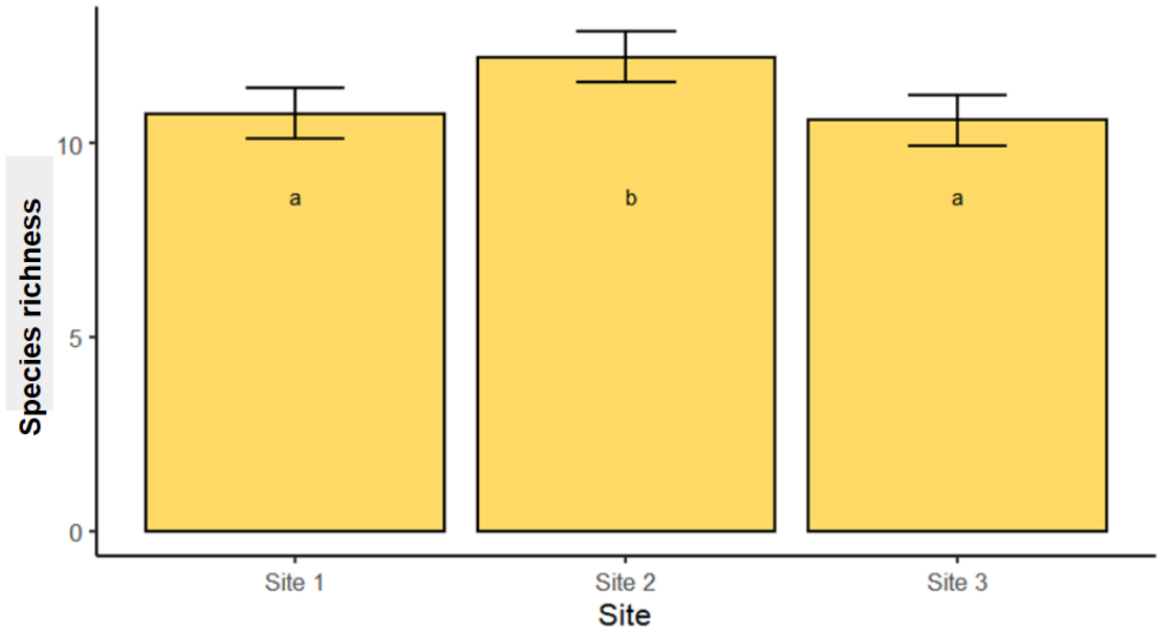

Figure 2.12: Species richness (emmean) at each individual site after 2 growing seasons post disturbance in Kenna Cartwright Park (± SE). Differences in letters within individual bars indicate significance groupings.

An NMDS was run for all 144 plots together while being compared to A) amendment treatments received, B) site locations of the plots, and C) seeding treatments received (Figure 2.13). There was no discernible difference in the vegetation makeup at each plot when grouped by seeding treatments or by amendment treatments received. However, there was a clear grouping of plots by the site they were located at. Showing that site has a discernible difference in the vegetation makeup, regardless of the seeding or amendment treatment the plots received.

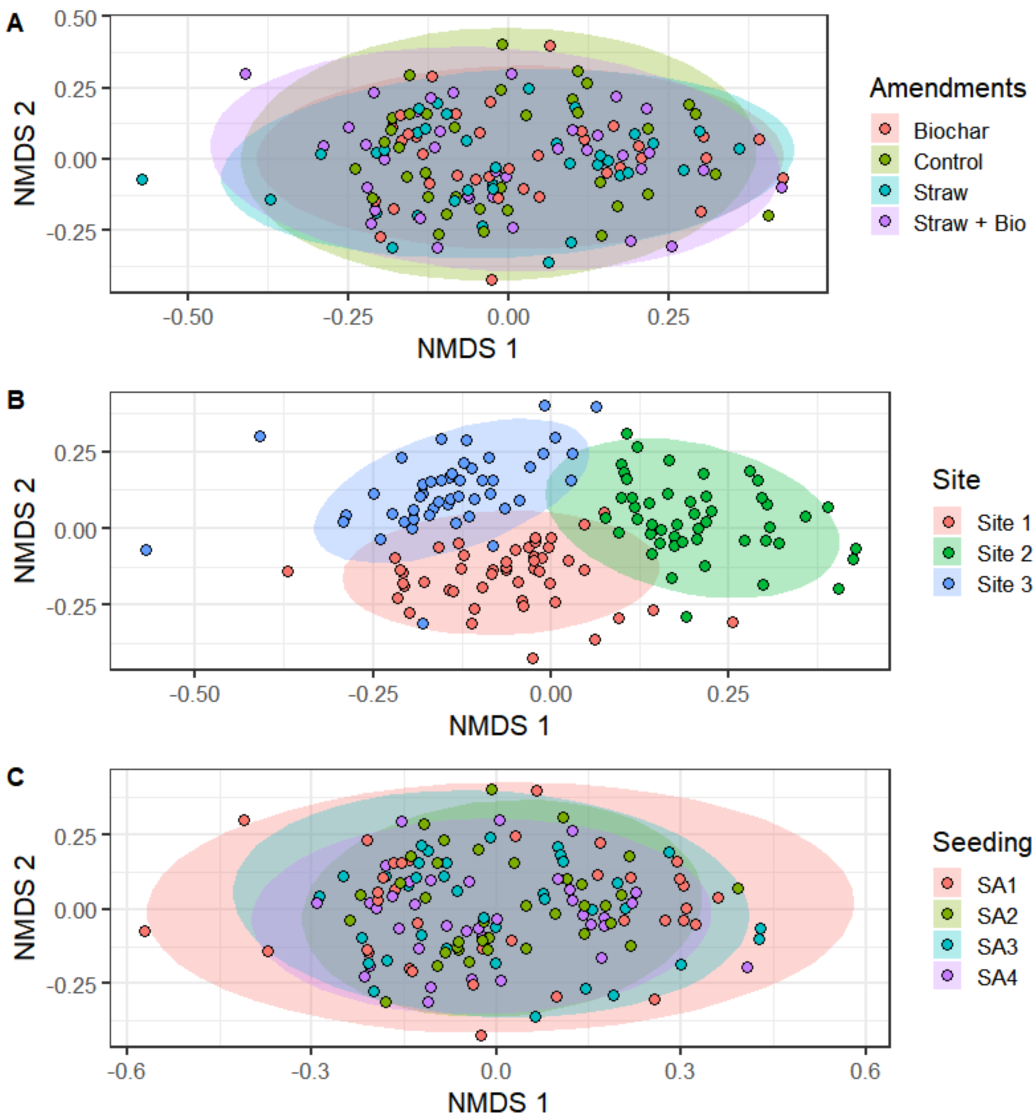

Figure 2.13: NMDS showing vegetation similarity of all 144 plots (48 plots and 3 different sites) when compared across factors A) amendments received, B) site location, and C) seeding treatment received.

An NMDS was run for all 144 plots, separated by sites, and being compared by the amendment treatment and seeding treatment received at each plot (Figure 2.14). For all three sites there is no discernible difference in vegetation similarity when plots are separated out by the amendment treatment received or the seeding treatment received.

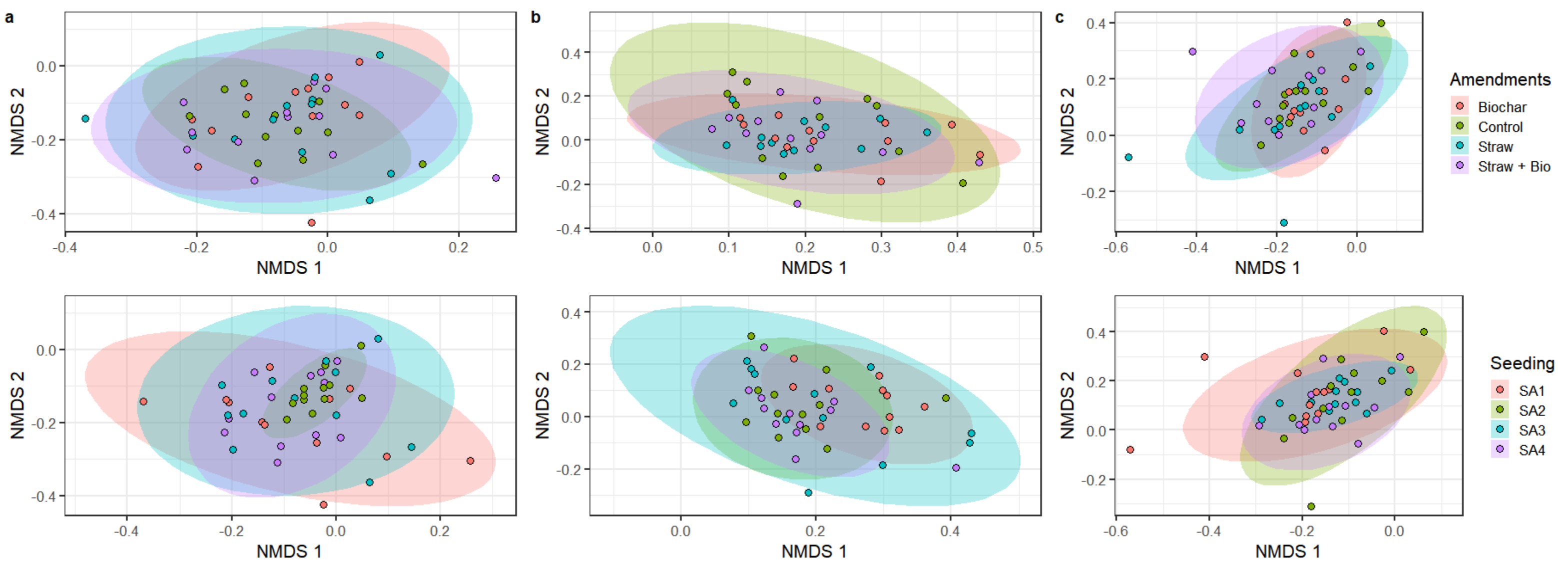

Figure 2.14: NMDS plots showing vegetation similarity separated by site (column a) Site 1 (top of the hill), column b) Site 2 (cellular tower), column c) Site 3 (bottom of the hill). Each site has the plot's vegetation similarity being compared to amendment treatments (top row) and seeding treatments (bottom row) received.

There is no significant effect caused by the amendment treatment plots received on % exotic coverage ($F_{3,96} = 0.243$, $p = 0.866$) (Figure 2.15a). There is no significant effect caused by the seeding treatments each plot received on % exotic coverage ($F_{3,96} = 0.235$, $p = 0.872$) (Figure 2.15c). However, site location of a plot had a significant effect on the % exotic coverage. There was a significantly higher amount of exotic coverage at sites 1 and 2 compared to site 3 (Figure 2.15b) ($F_{2,96} = 42.69$, $p < 0.001$). A list of scene exotics is shown in Appendix D.

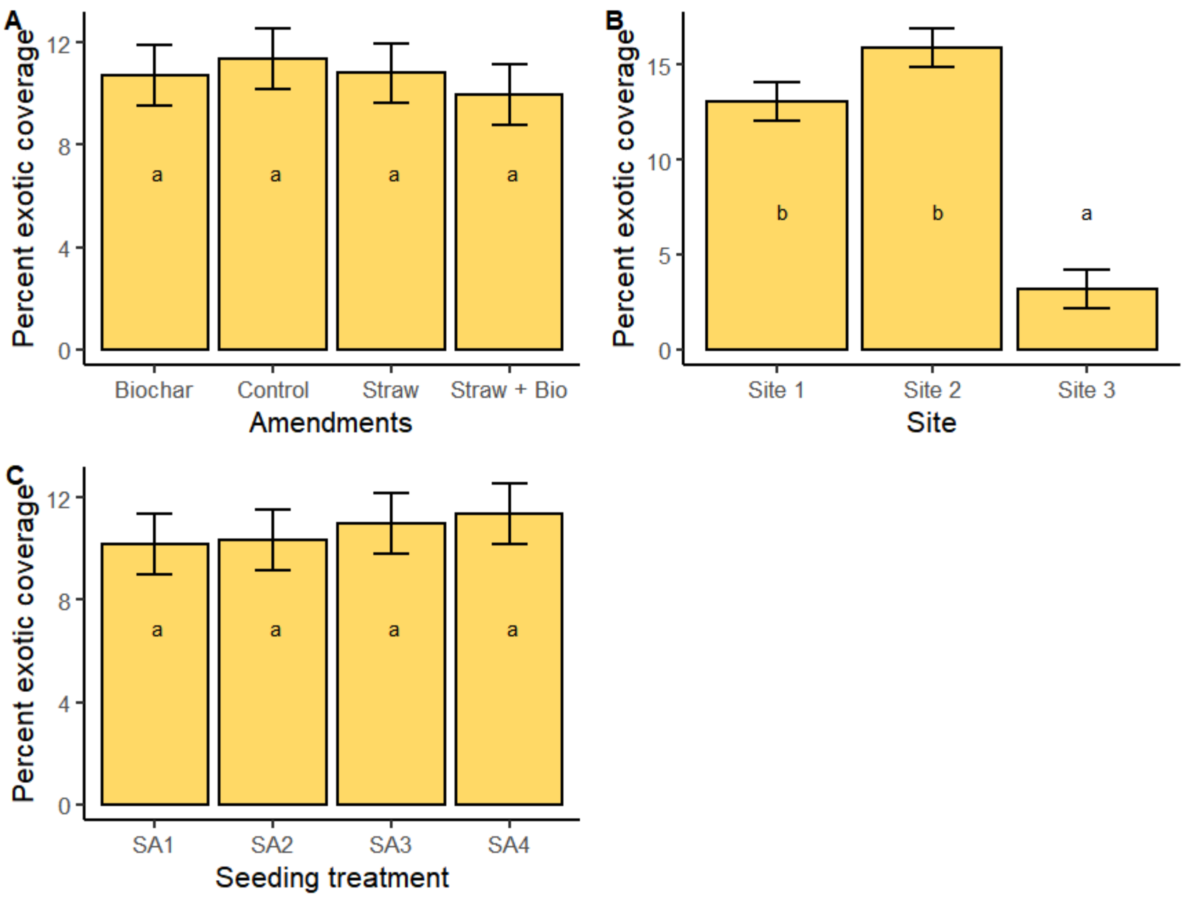

Figure 2.15: Percent cover of exotic species across factors of A) soil amendments, B) site, and C) seeding groups received. Differences in letters within individual bars indicate significance groupings (± SE).

Multispectral Imagery Results

The means of each plot's multispectral values, averaged out by site, were compared to each other. Each site's GNDVI value was significantly different from each other (Table 2.6). While LCI, NDRE, and NDVI values were significantly larger at site 1 when compared to sites 2 and 3 (Table 2.3). OSAVI was not significantly different across any of the sites (Table 2.3).

Table 2.3: Mean value for five multispectral indices (GNDVI, LCI, NDRE, NDVI, and OSAVI) at the three research sites. Italicized values with an asterisk are significant at a 0.05 interval. Letters above italicized values show significance groups at a 0.05 interval.

Site	**GNDVI**	**LCI**	**NDRE**	**NDVI**	**OSAVI**
Site 1	*0.424*^{a}	*0.156**	*0.124**	*0.404**	0.160
Site 2	*0.361*^{b}	0.111	0.092	0.288	0.158
Site 3	*0.322*^{c}	0.095	0.082	0.240	0.148
F-Value	$F_{2,96} = 68.86$	$F_{2,96} = 61.54$	$F_{2,96} = 55.39$	$F_{2,96} = 80.73$	$F_{2,96} = 1.73$
P-Value	<0.001	<0.001	<0.001	<0.001	0.183

The means of the multispectral indices GNDVI, LCI, NDRE, NDVI, and OSAVI at each site when plots are separated by the amendment treatment they received. Among the five indices there was no significant difference between the amendment treatments at each site (Table 2.4).

Table 2.4: Mean value for five multispectral indices (GNDVI, LCI, NDRE, NDVI, and OSAVI) at the three research sites when compared to the amendment treatments each individual plot received. An F-test was run to compare interaction effects of site and amendment treatment each plot received.

Site	**Amendment**	**GNDVI**	**LCI**	**NDRE**	**NDVI**	**OSAVI**
Site 1	Control	0.442	0.166	0.131	0.415	0.159
Site 1	Straw	0.424	0.157	0.124	0.399	0.161
Site 1	Biochar	0.421	0.151	0.119	0.403	0.162
Site 1	Straw + Bio	0.411	0.152	0.120	0.401	0.159
Site 2	Control	0.345	0.104	0.090	0.255	0.163
Site 2	Straw	0.341	0.098	0.084	0.253	0.165
Site 2	Biochar	0.348	0.087	0.075	0.243	0.146
Site 2	Straw + Bio	0.295	0.081	0.071	0.213	0.135
Site 3	Control	0.338	0.107	0.092	0.256	0.157
Site 3	Straw	0.309	0.103	0.089	0.247	0.152
Site 3	Biochar	0.295	0.099	0.085	0.247	0.134
Site 3	Straw + Bio	0.276	0.091	0.079	0.224	0.133
F-Value		$F_{6,96} = 1.03$	$F_{6,96} = 0.31$	$F_{6,96} = 0.35$	$F_{6,96} = 0.39$	$F_{6,96} = 0.69$
P-Value		0.411	0.927	0.906	0.882	0.661

The means of the multispectral indices GNDVI, LCI, NDRE, NDVI, and OSAVI at each site when plots are separated by the seeding treatment they received were compared using a two-way ANOVA. LCI and NDVI mean values at plots receiving the SA4 treatment within site 1 were both significantly larger than plots receiving the SA2 treatment within site 1 (Table 2.5). GNDVI, NDRE, and OSAVI were not significant (Table 2.5).

Table 2.5: Mean value for five multispectral indices (GNDVI, LCI, NDRE, NDVI, and OSAVI) at the three research sites when compared to the seeding treatments each individual plot received. An F-test was run to compare interaction effects of site and seeding treatment each plot received. Italicize values with an asterisk are significant at a 0.05 interval.

Site	**Seeding**	**GNDVI**	**LCI**	**NDRE**	**NDVI**	**OSAVI**
Site 1	SA1	0.337	0.124	0.098	0.320	0.125
Site 1	SA2	0.322	0.102	0.084	0.265	0.133
Site 1	SA3	0.350	0.134	0.104	0.346	0.125
Site 1	SA4	0.350	*0.140**	0.109	*0.363**	0.129
Site 2	SA1	0.262	0.073	0.064	0.182	0.113
Site 2	SA2	0.259	0.078	0.067	0.199	0.125
Site 2	SA3	0.279	0.074	0.064	0.201	0.130
Site 2	SA4	0.261	0.072	0.063	0.190	0.120
Site 3	SA1	0.299	0.096	0.084	0.227	0.135
Site 3	SA2	0.249	0.082	0.071	0.198	0.125
Site 3	SA3	0.225	0.074	0.065	0.184	0.100
Site 3	SA4	0.326	0.109	0.093	0.271	0.160
F-value		$F_{6,96} = 1.51$	$F_{6,96} = 2.35$	$F_{6,96} = 2.204$	$F_{6,96} = 2.28$	$F_{6,96} = 0.901$
P-Value		0.184	0.037	0.049	0.043	0.49

Soil Analysis Results

There was a significant difference in percent soil organic matter between plots that received a biochar amendment treatment versus a straw amendment treatment. However, plots receiving the control treatment or the straw + biochar treatment had no significant difference ($F_{3,96} = 2.88$, $p = 0.039$) (Table 2.6). There was a statistically significant difference in percent soil organic matter found in plots based on site location ($F_{2,96} = 3.29$, $p = 0.042$) (Table 2.6). However, the post-hoc model showed no significant difference in percent soil organic matter found in plots based on site location. The levels of interaction between amendments and seeding explain significant variance of the species richness. However, the number of pairwise comparisons are enormous which lead to a non-significant post-hoc (Appendix C.3).

Table 2.6: Mean percent soil organic matter (± SE) when compared across amendments and sites.

Amendments	Mean % Soil OM	Group
Straw	7.47 ± 0.47	a
Control	7.57 ± 0.47	ab
Straw + Bio	7.81 ± 0.47	ab
Biochar	8.37 ± 0.47	b

Site	Mean % Soil OM	Group
Site 1	8.04 ± 0.41	a
Site 2	7.99 ± 0.41	a
Site 3	7.37 ± 0.41	a

The plots that received the straw + biochar amendment treatment had a significantly higher percent soil moisture than the plots that received the control amendment treatments. While the plots that received either the biochar amendment treatment or the straw amendment treatment had no difference between soil moisture ($F_{3,96} = 3.2082$, p = 0.02651) (Table 2.7). Plots that were found in site 1 showed a significantly higher amount of percent soil moisture when compared to sites 2 and 3 ($F_{2,96} = 80.31$, $p < 0.001$) (Table 2.7).

Table 2.7: Mean percent soil organic moisture (± SE) when compared across amendments and sites.

Amendments	Mean % Soil Moisture	Group
Control	2.77 ± 0.28	a
Biochar	2.95 ± 0.28	ab
Straw	2.98 ± 0.28	ab
Straw + Bio	3.37 ± 0.28	b

Site	Mean % Soil Moisture	Group
Site 1	4.28 ± 0.24	b
Site 2	2.24 ± 0.24	a
Site 3	2.55 ± 0.24	a

Plots receiving the straw + biochar amendment showed a significantly higher soil pH than plots receiving the control treatment or the straw treatment. Plots that received the biochar treatment showed a significantly higher pH than the plots receiving the straw amendment treatment. While plots that received the straw amendment treatment or the control amendment treatment had no significant difference in pH when compared to each other ($F_{3,96} = 4.94$, $p = 0.003$) (Table 2.8). Plots found in site 2 had a significantly higher pH than plots found in site 3, and plots found in site 1 had no significant difference in pH when compared to sites 2 or 3($F_{2,96} = 3.80$, $p = 0.026$) (Table 2.8).

Table 2.8: Mean soil pH (± SE) when compared across amendments and sites.

Amendments	Mean Soil pH	Group
Straw	6.84 ± 0.05	a
Control	6.86 ± 0.05	ab
Biochar	6.95 ± 0.05	bc
Straw + Bio	6.96 ± 0.05	c

Site	Mean Soil pH	Group
Site 1	6.91 ± 0.05	ab
Site 2	6.95 ± 0.05	b
Site 3	6.86 ± 0.05	a

Elemental Results

When the soil nitrogen levels are compared by the amendment treatment received at each plot, there is no difference in mean soil nitrogen ($F_{3,96} = 0.515$, $p = 0.673$) (Table 2.9). However, when soil nitrogen levels are compared by the site each plot was located in there is a difference. Site 2 had the highest soil nitrogen levels and site 1 had the lowest soil nitrogen levels ($F_{2,96} = 32.769$, $p < 0.001$) (Table 2.9).

Table 2.9: Mean soil nitrogen levels (± SE) when compared across amendments and sites.

Amendments	Nitrogen	Group
Straw	0.186 ± 0.012	a
Control	0.194 ± 0.012	a
Biochar	0.193 ± 0.012	a
Straw + Bio	0.197 ± 0.012	a

Site	Nitrogen	Group
Site 1	0.154 ± 0.011	a
Site 2	0.217 ± 0.011	b
Site 3	0.174 ± 0.011	c

When the soil carbon levels are compared by the amendment treatment received at each plot, there is no difference in mean soil carbon ($F_{3,96} = 0.885$, $p = 0.452$) (Table 2.10). When soil nitrogen levels are compared by the site each plot was in there is no difference ($F_{2,96} = 2.796$, $p = 0.066$) (Table 2.10).

Table 2.10: Mean soil carbon levels (± SE) when compared across amendments and sites.

Amendments	Carbon	Group
Straw	2.58 ± 0.27	a
Control	2.72 ± 0.27	a
Biochar	2.82 ± 0.27	a
Straw + Bio	2.88 ± 0.27	a

Site	Carbon	Group
Site 1	2.69 ± 0.24	a
Site 2	2.97 ± 0.24	a
Site 3	2.59 ± 0.24	a

DISCUSSION

Priority advantage was different based on planting order and site location, LS species showed a more positive priority value compared to the ES species. Plots receiving both straw and biochar as an amendment had higher pH, percent soil moisture, and percent organic matter. Site specificity played a major role in the results of this study. The highest species richness and percent moisture was at site 1, while site 2 had the highest exotic cover, and site 3 had the lowest percent exotic cover.

Priority Effects

I found that priority effects were based on site characteristics, as much as it was based on the species. LS species tended to have a more positive priority value than ES species. However, this result was species dependent. The species with the most positive priority value was an ES grass species, Sandberg's bluegrass. As well as site dependent, site 1 had the most positive priority value. This trend continued when considering the individual species' priority response at site 1. The LS species exhibited a more positive priority value at site 1 than many of the ES species but showed similar priority results as the ES species at sites 2 and 3 (Figure 2.3), giving context as to why their overall priority value is more positive than ES species.

Looking at the priority value of LS species we must acknowledge that arrowleaf balsamroot appeared not to establish and was absent in all plots. The lack of colonization of arrowleaf balsamroot may be due to two factors: 1.) *Balsamorhiza sagittata* has been noted to have a poor record for colonizing and establishing itself in recently disturbed environments (Gucker and Shaw 2018); and 2.) *Balsamorhiza sagittata* seeds need two to three months of cold and wet stratification to help break dormancy, and even when given these treatments *Balsamorhiza sagittata* has a low germination percentage (Young and Evans 1979, Kitchen and Monsen 1996, Chambers et al. 2006). Due to the latter, I expected to find an increase in germination after a natural cold stratification period during the 2021-2022 winter season but did not seem to occur. *Balsamorhiza sagittata* is a typical indicator species of a near climax environment (Tisdale 1947, Rumsey 1971, Franklin and Dyrness 1973), therefore germination would have indicated that the treatment was trending towards a climax environment.

Blanket flower had a strongly negative priority value in sites 2 and 3, but a positive priority value at site 1, with a priority value around 0.5. This means at site 1 blanket flower benefited from being seeded second. I think this may be due to the ability of forbs to establish more predominantly in the ponderosa pine biogeoclimatic zone.

The idea of whether one of the seeded plants is better suited for being seeded first or second becomes more convoluted when looking at the ES planting group. This planting group included blanket flower, Sandberg's bluegrass, slender wheatgrass, and western yarrow. The ES planting group had a priority value near -0.5, which means this group significantly benefited from being seeded first at a site compared to the LS planting group.

Slender wheatgrass and western yarrow showed a negative priority value across all three sites (Figure 2.3). I expected most species would show significantly higher amounts of growth when planted first due to having the time to sequester nutrients and water without much competition, the ability to grow without having to compete for space, and the potential to establish themselves in a newly disturbed environment before other species (Dickson et al. 2012, Sarneel 2016, Yu et al. 2020). Therefore, slender wheatgrass and western yarrow confirmed my expectation by accumulating more biomass when seeded first.

The priority value of Sandberg's bluegrass was positive at all three sites, which means that it benefited in growth when planted second. This could be due to its ability to be a competitive grower, especially after a disturbance event (Davies et al. 2007, Bates et al. 2009). However, I expected it to have a rapid growth when seeded first directly after the disturbance occurs, not when it was seeded after prior establishment of a founding plant community. One potential reason is that Sandberg's bluegrass has been found to be a stronger interspecific competitor, rather than an intraspecific competitor (Mangla et al. 2011). Referencing our results, this could mean that Sandberg's bluegrass has a stronger growth response in the field in the face of competition. The reason behind this could potentially be due to some unknown biotic or abiotic factors occurring in the environment after establishing; a specific facultative relationship that is occurring between Sandberg's bluegrass and fescue; or some other voluntary that arrives before our seeding of Sandberg's bluegrass.

Deterring Exotic Growth

A major concern in any restoration project, especially in an environment that recently experienced a major disturbance event, is the removal and continued deterrence of exotic and exotic species (Pysek and Richardson 2008, Dickson et al. 2012). This concern holds true in the interior grasslands of British Columbia as there are numerous exotic species that can outcompete native species (Mack 2011, Invasive Species Council of British Columbia 2022, Singh et al. 2022).

This project examined a few potential ways of assisting natives outcompete exotic species. Amendments were used to control the growth of the exotics, seeding regiments to help natives grow by using their growth characteristics, and arrival patterns to promote native growth, deter, and outcompete exotic species.

Four different amendment treatments were used to help prevent establishment and growth of exotic species. I expected a decrease in exotic coverage at the plots that received the straw matting amendment treatment. Despite my expectation, all four treatments did not create any significant decrease in exotic coverage.

The lack of decrease in exotic species could be due to a few reasons, the first being that there was already a considerable number of exotic seeds present in the seed bank, which would have affected each plot similarly. Yet, even when a seed bank trial was run using soils from the field sites, I did not find any exotic species in those trials. Another reason for these findings is because there was not enough time for the amendments to control the exotic species. Lastly, this could simply be because the amendments had no significant effect over the amount of growth from the exotic species.

I also tested the effect seeding patterns may have on exotic growth and coverage. The idea behind this was to use priority effects to allow native species to establish a recently disturbed ecosystem, sequester nutrients, and outcompete arriving exotic species (Mwangi et al. 2007, Dickson et al. 2012, Yu et al. 2020). However, across all four seeding treatments, there was no significant decrease in exotic coverage.

One reason for no difference in exotic coverage is due to the significant presence of exotic seeds in the seed bank (Newsome and Noble 1986, Lonsdale et al. 1988, Baskin and Baskin 1998). But, as previously stated, no exotic species germinated during seedbank trials. Another reason for these results is that the seeding treatments were not given enough time to show a significant difference in exotic coverage - this idea will be further discussed later in this chapter. Lastly, there may be no significant difference in the seeding treatment’s ability to decrease the growth of exotic species.

As far as percent exotic cover by site, there was significantly higher exotic cover at sites 1 and 2, while site 3 had the least amount of exotic cover by a significant margin. I think this has to do with site characteristics, site 3 being in the bunchgrass biogeoclimatic zone allowing for an increase in establishment by seeded grasses.

Effects of Soil Amendments on Restoration Success

Across all major soil indices, pH, soil moisture, and organic matter, there were significant differences with respect to the four different soil amendment treatments (straw, biochar, straw + biochar, and the control).

Plots treated with a straw matting amendment had the lowest percent of soil organic matter, with a mean across all sites of 7.47%. However, this was only significantly different from plots receiving biochar alone. Plots treated with straw matting had a mean soil moisture percentage of 2.98% which also was not significantly different from the control. Lastly, plots receiving straw matting had a mean soil pH of 6.84, which was also not significantly different from the control. These results show straw matting alone does not significantly change soil characteristics over two growing seasons. We can make sense of most of these results, as soil remediation was not the reason behind straw mattings use. Straw matting ideally helps to maintain soil structure and deter weedy growth (Steinfeld et al. 2007). However, I did not observe a significant decline of exotic, non-native plants on plots with straw matting compared to control plots.

Plots treated with biochar had the highest percent of soil organic matter, 8.37%. When looking at mean soil moisture plots treated with biochar, soil moisture percentage was 2.95%, which was also not significantly different from the control plots. This result contradicts other research suggesting that biochar increases soil moisture (Jeffery et al, 2011, Novak et al. 2012, Basso et al. 2013, Masiello et al. 2015, Haider et al. 2017). The timing of my measurements, or the fact that my site location was in a semi-arid environment, may have influenced these results. It is possible that, over time, biochar treated plots may experience an increase in soil moisture and plant available water. Plots treated with biochar had an average pH of 6.95, which is not significantly different from the control. This may suggest that biochar had no significant effect over the soil characteristics of a site. However, the introduction of soil nutrients by biochar can take time (Lal 2008, Sohi et al. 2010). In addition, many of the benefits of biochar introduction are not measured in this study, including carbon sequestration (Lal 2008, Sohi et al. 2010), increased soil structure (Cao et al. 2009, Chen and Chen 2009), and an increase of soil microbial biomass and enzymatic activities (Smith et al. 2010, Jones et al. 2011, Lehmann et al. 2011).

Plots treated with both straw matting and biochar as amendments had a mean soil organic matter percentage of 7.81%, which was not significantly different from the control. However, the mean soil moisture percentage was significantly different from the control at 3.37% soil moisture. I believe the increase in soil moisture on these plots is due to a combination of the ability of biochar to retain water and the shading affect that straw matting may have had on the soil. This suggests that both biochar and straw matting are needed in the short term to increase a site's soil moisture. The mean soil pH at plots treated with both amendments, with an average pH of 6.96, was also significantly different from the control.

It should be noted that, in terms of the immediate effect the soil amendment treatments had on the Shannon diversity, there was no significant effect after two years. This holds true when the soil amendments were compared across both sites and seeding treatments across plots. However, literature suggests that a plot with healthy soil have an increase in plant diversity, plant growth, and plant nutrient uptake (Kirankumar et al. 2008, Cummings 2009, Guinazu et al. 2009).

In terms of soil health the percent organic matter and percent soil moisture results may suggest that treating plots with both straw matting and biochar amendments is best in the short term. This is especially consequential for sites being restored where the restoration manager, or company overlooking the restoration, may prefer this method as it has the most immediate effects on soil health. This could lead to a healthier, more streamlined restoration of the disturbed site for the years to follow.

Site Difference Role in Success of Restoration

As discussed briefly, restoration is site specific (Bakker et al. 2003, Grman et al. 2013.), even when sites are as close together as the research sites in my study. The three sites used in this project were all located in different biogeoclimatic zones, with different site history and site characteristics. Factors such as these will affect the success of a restoration projects and should be considered (Kuussaari et al. 2009, Brudvig and Damschen 2010, De Souza Leite 2013, German et al. 2013). Site-specific characteristics play out in the implementation of my restoration treatments and the outcomes observed.

The specific site difference is apparent when looking at the soil characteristic indices. Both mean percent soil moisture and mean soil pH show that there were significant differences between the sites. Site 1 had the highest mean percent soil moisture of 4.28%. This result is likely due to site 1 being in the Ponderosa Pine biogeoclimatic zone and having a denser tree canopy and being higher in elevation causing a decrease in temperature and an increase in moisture. While site 2 had the highest soil pH of 6.95, and site 3 had the lowest of 6.86.

My NDVI results showed that the SA4 seeding treatment in site 1 had a significantly higher NDVI value, suggesting this treatment and site combination showed a higher amount of greenness compared to the rest of the plots. This is backed up by the LCI value also being significantly higher at plots in site 1 receiving the SA4 seeding treatment, indicating a higher amount of chlorophyll content at these plots. However, these results could have occurred due to a type-1 error, a false-positive.

The effects of site characteristics had an effect on priority effects and exotic coverage. At site 1, priority value was near zero, which is the highest priority value at any of the sites, while site 2 had the lowest priority value, around -0.5. A near zero priority value means that regardless of our arrival order, an individual species (in this case the planting group) will have a similar amount of growth, regardless of the time of arrival in the ecosystem. Percent exotic coverage was also significantly different between sites, with site 3 having the least amount of exotic coverage compared to site 1 and 2. This may be due to site 3 being in the bunchgrass biogeoclimatic zone, meaning that grasses seeded would have a much better chance of competing at this site due to it being in a biogeoclimatic zone more suited for their growth. It could also be due to site 3 being much drier, thus reducing the recruitment of species.

Knowing a recently disturbed site's soil characteristics, site specific characteristics, and potential plant community structure can help restoration managers decide what methods may be best to help restore a site. Having this knowledge will allow managers to save time, energy, and money while leading to more successful restoration projects.

Restoration Projects Timelines and Long-term Site Management

Restoration of a disturbed site back to the post disturbance reference can take years to accomplish. For a restoration project to start showing major changes it can take up to 3-6 years of management, depending on site and level of disturbance that occurred (Stromberg et al. 2007, Hedberg and Kotowski 2010, Rehounkova et al. 2021). For many native grasses it takes at least three growing seasons to fully establish themselves under ideal conditions (Bugg et al. 1997). This timeline does not include the possibility of weedy exotics being present in the environment.

Knowing it can take many years for a restoration project to show significant progress, along with the limitations of this project being conducted over one year, we can begin to explain some insignificant results that were found.

For species richness, after one year, there was no significant difference between our treated plots and control plots. This also included the amendment treatments having no significant difference of exotic coverage versus the control plots. These results can be expected to change over the next few growing seasons as the native species have more time to establish themselves and the potential benefits of the amendments start to actualize. In addition to the native establishment, I expect the amendments (namely the straw matting amendment) to control further growth and establishment of weedy exotic species.

I can also expect to an effect of the seeding and amendments treatments each plot received on the plant community composition, when compared to the control. After a year of growth, when looking at the NMDS graphs for both amendments and seeding, there was no discernible difference in plant community composition. I expected these factors to have an effect and show a difference compared to the control plots, especially for the different seeding treatments. This observation still holds true when the plots are separated out by their sites. As previously stated, grass establishment can take upwards of 3 years, meaning that the full effects of the seeding treatments may only be seen after two additional growing seasons.

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CHAPTER 3: THE IMPORTANCE OF PRIORITY EFFECTS AND NUTRIENT LEVELS FOR SEMI-ARID GRASSLAND PLANT COMMUNITY DYNAMICS

INTRODUCTION

Priority effects occur when the arrival order and timing of the germination rate and seedling rates of plants in an ecosystem can affect long term community structure (Erikkson and Erikkson 1998, Yu et al 2020). In a newly colonized ecosystem, early arriving plants will have a competitive advantage over plants that arrive later (Erikkson and Erikkson 1998, Sarneel 2016, Ploughe et al. 2020, Yu et al. 2020).

Priority effects affect the interactions between species but may take multiple growing seasons to show significant results due to abiotic and biotic variables, thus they can be hard to quantify and control. Factors such as abnormal rainfall and lack of water (Slatyer 1974, Brown 1977, Risser 1985), extreme temperatures (Cooper and Tainton 1968, Burke et al. 1976, Berry and Bjorkman 1980, Hatfield and Prueger 2015), grazing (Hyder 1972, Mcshane and Sauer 1985, Eckert and Spencer 1987, Caldwell 2021), lack of plant response to arbuscular mycorrhiza (Berger and Gutjahr 2021), and competitive interaction with exotics, voluntary flora, and other sown seeds (Christie and Detling 1982, Fowler 1986) can impact and influence priority effects.

Exotic plants can dominate plant communities due to their competitive ability such as faster growth, greater fecundity, and higher seedling survival rates and establishments (Pysek and Richardson 2008). Exotic species' plant traits that confer rapid dispersal and early arrival in disturbed ecosystems are conducive to enhanced priority effects and therefore may confer the ability to provide a competitive advantage of exotic species compared to native flora. When exotics establish themselves before natives they tend to form monocultures and reduce the occurrence and above ground productivity of natives, while diversity increases when natives are able establish first (Abraham et al. 2008, Stevens and Fehmi 2011, Dickson et al. 2012). The ability to establish earlier in the growing season and quickly sequester available nutrients and water allows non-native exotic plants, in particular spotted knapweed (*Centaurea stoebe*), to take over recently disturbed semi-arid grasslands (Pysek and Richardson 2008, Dickson et al. 2012).

The timing of arrival of plants during succession has an impact on community assembly, and this can also affect the fertility of the soil that the plants are arriving in. It has been suggested in high nutrient ecosystems that plants that arrive first tend to sequester the nutrients and preempt light resources, not allowing for the successful establishment of plants that arrive after (Kardol et al. 2012).

Previous greenhouse research has been done regarding priority effects in a riparian ecosystem, showing that priority effects changed depending upon the level of soil wetness (Sarneel 2016). Dickson et al. (2012) found diversity increased when one native species was sown 3 weeks prior to exotic species, but exotic plants emitted a stronger priority effect than native plants when seeded first. Von Gillhaussen et al. (2014) found the arrival order of plant functional groups (grasses, forbs, and legumes) had a significant effect on aboveground biomass. Ploughe et al. (2020) found that the earlier an exotic species establishes in an ecosystem, the stronger the priority effects emitted by the exotic will be and the establishment of native species will be lessened.

The purpose of this study was to examine how native forbs and grasses from the British Columbia grasslands will interact with each other when arrival order is manipulated under various levels of fertilization and how an established grassland community is affected by invasion under ideal growing conditions. This information will provide a clearer understanding of the interactions these forbs and grasses have with each other, how priority effects affect their growth, how priority effects change under differing fertilization regiments, and what sowing order leads to the highest diversity and total biomass while at the same time deterring exotic exotics. The information provided will lead to a better understanding of how arrival order and priority effects can be used to restore sites and deter exotic growth.

Objectives

1) Test the effects of different sowing orders among native plants without competition from exotic and voluntary species and in the face of competition from exotic species (spotted knapweed).

2) To identify what sowing order has the highest amount of above and below ground biomass among native species and deters the most amount of exotic growth.

3) Evaluate which planting order leads to the highest amount of diversity and richness among native species.

4) Examine differing fertilizer levels effect on soil health.

Predictions

I hypothesize that the pots that experience the planting of the early successional grasses and forbs at the same time as the late successional grasses and forbs will have the highest amount of productivity, but lower diversity. While the pots that experience the sowing of the late successional grasses and forbs four weeks prior to the early successional grasses and forbs will have the lowest amount of productivity, but higher diversity across the different fertilizer levels. Additionally, I think that the higher fertilizer levels will produce a higher amount of productivity and lower amount of diversity across the different planting orders.

When concerning the ability of the plant community to deter the exotic growth of spotted knapweed I think the pots that experienced the planting of the early successional grasses and forbs at the same time as the late successional grasses and forbs with a low amount of fertilizer will be able to deter exotic species best. I think this will be due to both early and late successional plants having more time to establish themselves in the pot and sequester the available nutrients. While the pots that experience the sowing of the late successional grasses and forbs four weeks prior to the early successional grasses and forbs will have a more challenging time deterring the invasion of spotted knapweed across all fertilizer levels. I think this will be due to the inability of the late successional species to quickly establish themselves and sequester enough of the available nutrients and the early successional grasses and forbs not having enough time to fully establish themselves before the invasion of the spotted knapweed.

Finally, using the priority strength formula, outlined by Sarneel (2016), I hypothesize that early successional grasses and forbs will emit a stronger priority over the late successional grasses and forbs. My reasoning behind this is that early successional species can sequester nutrients and water easier than late successional species.

METHODS

Study Design

The study aimed to look at the effects of sowing order on the biomass and composition of native successional species, as well as the effects of various levels of fertilizer on the biomass of native plant mixtures. This study also had an invasion component that was conducted after the native species had time to establish themselves. This was done to analyze the ability of the planting groups to resist invasion by spotted knapweed. An Osmocote © Smart Release slow-release fertilizer was used in different levels. The fertilizer had a nutrient breakdown of 15% nitrogen, 9% phosphate, and 12% potassium with micronutrients filling out the rest of the fertilizer.

Total Nitrogen (N)	15%
Available Phosphate (P_2O_5)	9%
Soluble Potash (K_2O)	12%
Magnesium (Mg)	1.30%
Sulfur (S)	6%
Boron (B)	0.02%
Copper (Cu)	0.05%
Iron (Fe)	0.46%
Manganese (Mn)	0.06%
Molybdenum (Mo)	0.02%
Zinc (Zn)	0.05%

Figure 3.1: Nutrients breakdown of the Osmocote © Smart-Release Plant Food Plus used in the priority effects study.

In the greenhouse, I used a randomized factorial design (Figure 3.2), with each treatment being replicated six times. There were two distinct levels of fertilizer used: a low fertilizer range that was applied at a rate of 4 g nitrogen/m^2, and a high fertilizer range that was applied at a rate of 10 g nitrogen/m^2 (You et al. 2017). A Kruskal Wallis Test was run on nitrogen levels found in the soil, post data collection, to confirm a difference between the fertilizer levels used (Appendix F). Using these rates of nitrogen per m^2 the amount of the fertilizer used in the low fertilizer pots was 2.96 g per pot and for the pots that had a high amount of fertilizer applied 7.4 g per pot was used.

There were three sowing treatments tested: 1) all seeds sown at the same time, 2) the early-successional species planted first then the late-successional species planted four weeks later, and 3) the late-successional species planted first then the early-successional species planted four weeks later. In addition to the different fertilizer levels and seed arrivals, spotted knapweed was introduced into some of the pots after 8 weeks of growth. Pots (16.5 cm in height, 17 cm in diameter) were filled with sand and were placed in an oven at 70°C for 48 hours to sterilize any potential seeds or seedlings found in the sand before sowing took place (Sinegani and Hosseinpur 2010).

The four soil amendments and three sowing treatments create a total of 12 different treatments. With each pot being replicated a total of 6 times this meant there were a total of 72 pots. In addition to the 72 pots there were also 12 control pots that will not be sown with any seeds, 6 of which had a low fertilizer level and 6 with a high fertilizer level. There were also 12 pots sown with spotted knapweed in week 8 of the trial to compare with the other pots to determine how well they were able to deter the growth of the spotted knapweed. Six of the pots had a low fertilizer level and 6 with a high fertilizer level. All the knapweed and no seeds sown pots were set up and watered just like the rest of the 72 pots at week 0. All combinations of treatments are in table 3.2.

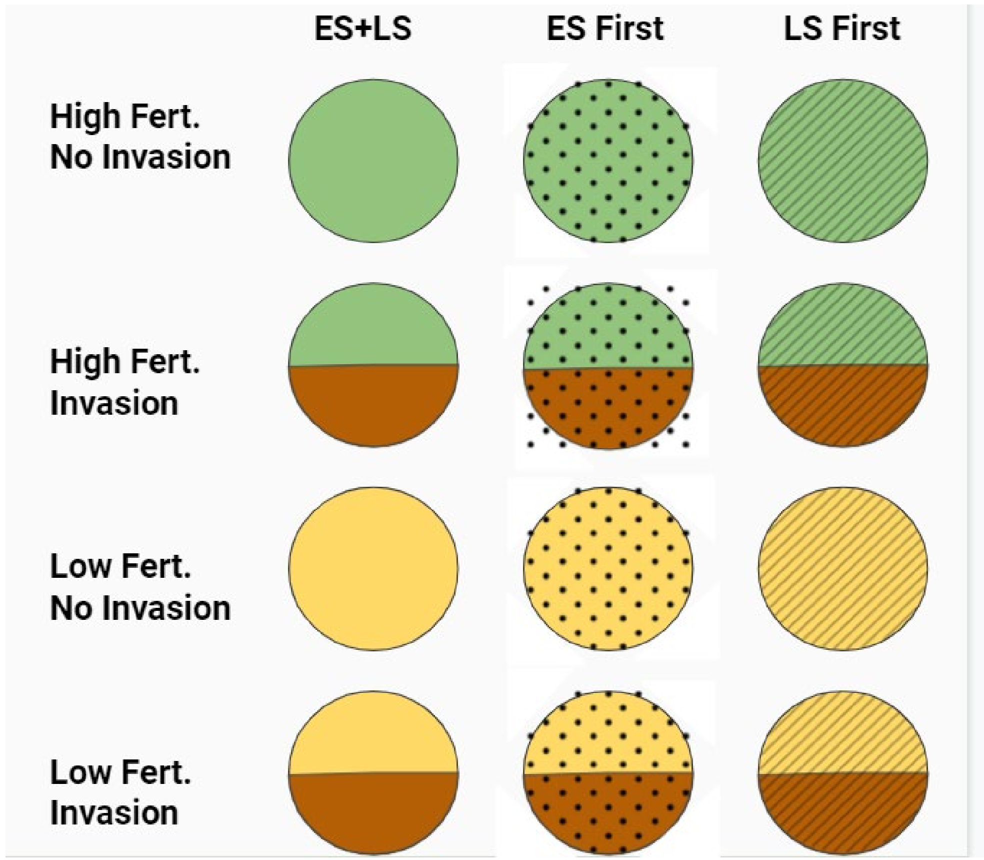

Figure 3.2: A schematic of the planting orders and amendment types used. ES represents the group of early successional grasses and forbs, while LS represents the group of late successional grasses and forbs. The trial contained 6 replicates of each.

All plant species used in the greenhouse study were the same as the species used in the field study, except for *Asclepias speciosa* (showy milkweed) which replaced *Balsamorhiza sagittata* (arrowleaf balsamroot) (Table 3.1).

Asclepias speciosa (showy milkweed) is a forb native to British Columbia and is a mid-successional weedy species that can quickly colonize recently disturbed sites (Ulev 2005).

Table 3.1: List of native forbs and grasses used in the priority effects greenhouse trials.

#	**Common Name**	**Scientific Name**	**Type**	**Succession**
1	Blanketflower	*Gaillardia pulchella*	Native Forb	Early
2	Sandberg Bluegrass	*Poa secunda*	Native Grass	Early
3	Western Yarrow	*Achillea millefolium*	Native Forb	Early
4	Slender Wheatgrass	*Elymus trachycaulus*	Native Grass	Early
5	Rough Fescue	*Festuca campestris*	Native Grass	Late
6	Showy Milkweed	*Asclepias speciosa*	Native Forb	Late
7	Rocky Mtn. Fescue	*Festuca saximontana*	Native Grass	Late
8	Idaho Fescue	*Festuca idahoensis*	Native Grass	Late

Table 3.2: List of 12 unique treatments that can occur in the greenhouse trials which includes sowing treatments and soil amendments.

#	Sowing Treatment 1 (Week 0)	Sowing Treatment 2 (Week 4)	Invasion	Soil Amendment
1	Mix of Early and Late Successional	N/A	Yes	Low Fertilizer
2	Mix of Early and Late Successional	N/A	Yes	High Fertilizer
3	Mix of Early and Late Successional	N/A	No	Low Fertilizer
4	Mix of Early and Late Successional	N/A	No	High Fertilizer
5	Early Successional	Late Successional	Yes	Low Fertilizer
6	Early Successional	Late Successional	Yes	High Fertilizer
7	Early Successional	Late Successional	No	Low Fertilizer
8	Early Successional	Late Successional	No	High Fertilizer
9	Late Successional	Early Successional	Yes	Low Fertilizer
10	Late Successional	Early Successional	Yes	High Fertilizer
11	Late Successional	Early Successional	No	Low Fertilizer
12	Late Successional	Early Successional	No	High Fertilizer

Each pot was sown with their corresponding seed mix containing 35 viable seeds per plant. To calculate viable seed count a germination trial was conducted prior to the start of the experiment, the results of the trial can be seen in Appendix A. This count came out to be 140 total viable seeds per seeding group and 280 for the pots that received both the early and late successional seed mixes at week 0. At week 4 the pots that received the ES seed mix then received the LS seed mix, and the pots that received the LS seed mix then received the ES seed mix. The pots were watered twice a week to a volumetric water concentration of 15-20%, based on soil moisture data from soil collected in Kenna Cartwright Nature Park. To account for microclimates that may occur in the greenhouse, the pots placement in the greenhouse pod were re-randomized every 4 weeks. The complete timeline of events can be seen in figure 3.3 below.

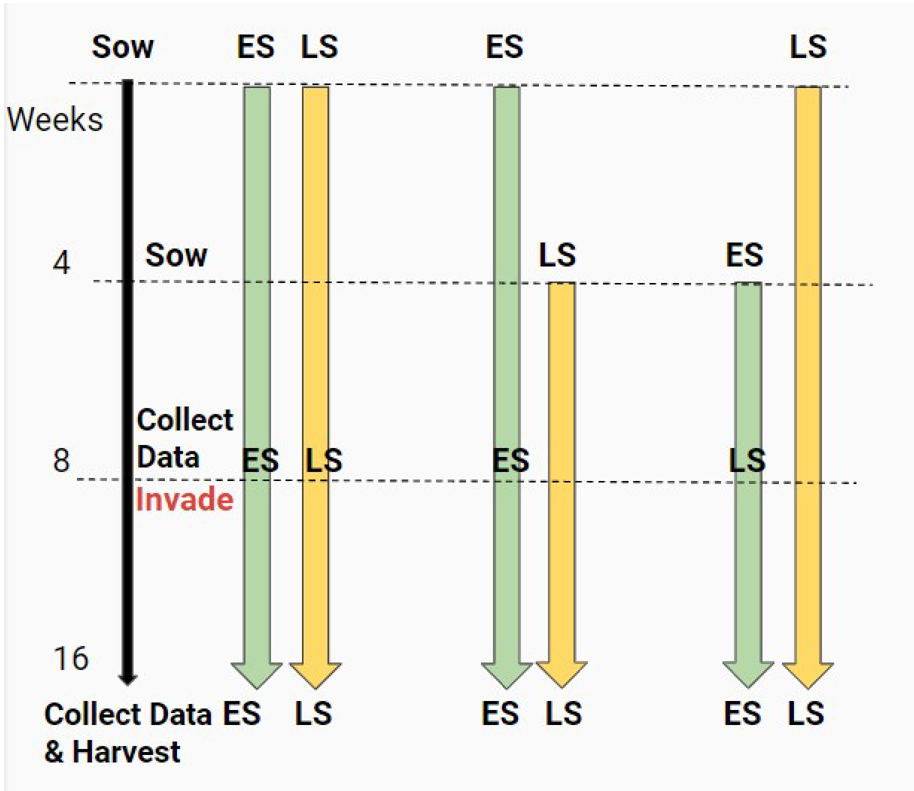

Figure 3.3: A detailed outline of the planting order time, when each group's seedlings will be measured, time of spotted knapweed invasion, and the time of seedling harvest. ES represents the group of early successional grasses and forbs, while LS represents the group of late successional grasses and forbs.

Conditions in the greenhouse were kept constant for the duration of the experiment using the Argus Controls software. The greenhouse was set to have a day cycle of 16 hours and a night cycle of 8 hours, the Argus Controls temperature range in the pods was set 25 to 28 degrees celsius between the time of 7 am and 10 pm every day and from 11 pm to 6 am the temperature was set between 22 and 25 degrees celsius. Between the hot and cool cycles there was a one-hour transition period, or "ramping" period, in which the temperature in the pod gradually increased or decreased to the desired temperature. The relative humidity of the pod was set between 40 and 55% from 11 am to 10 pm every day, and between 11 pm to 10 am the humidity was set between 70 and 85%. Between the two humidity levels there was a one-hour transitional period in which the humidity in the pod gradually increased or decreased to the desired humidity.

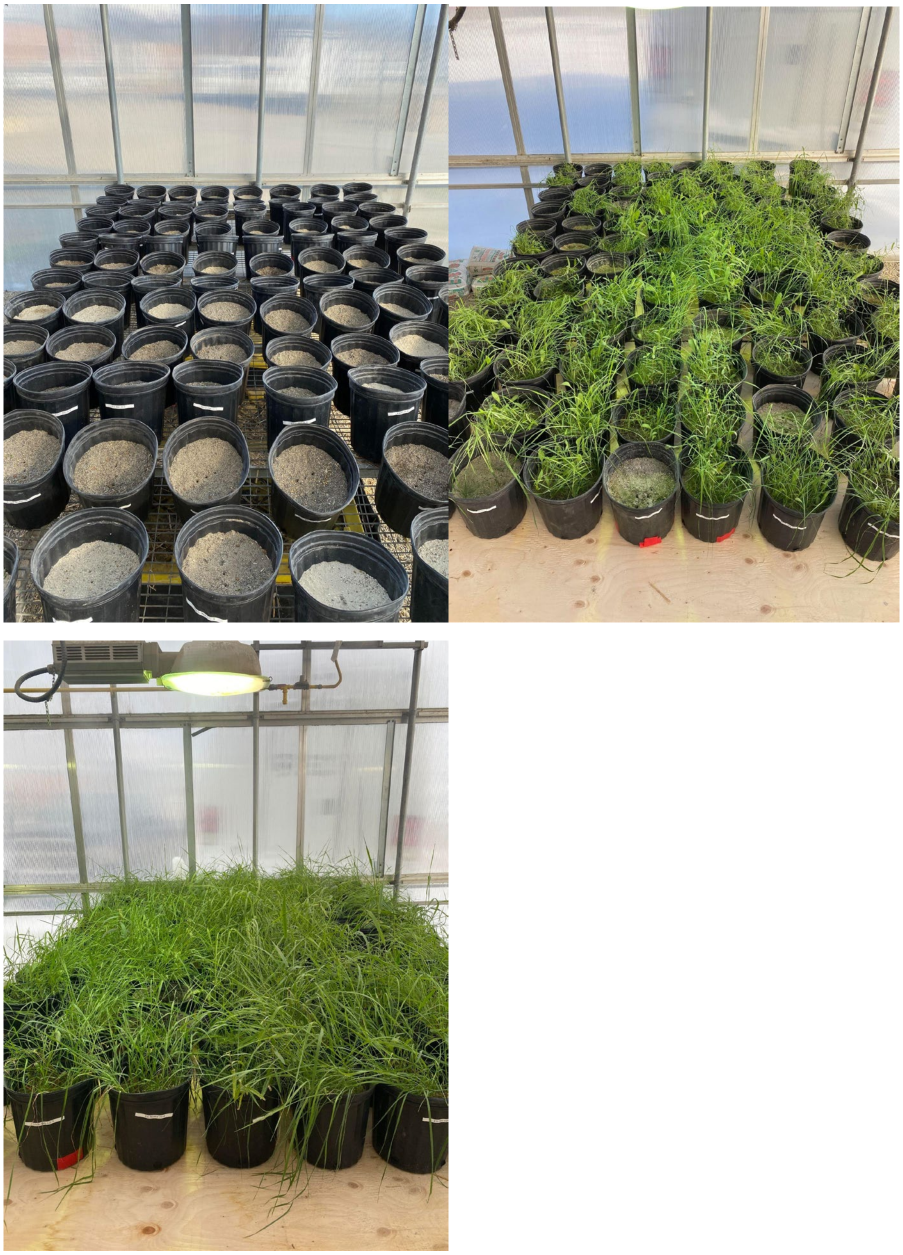

Figure 3.4: A photo of the trial pots at week zero, eight, and thirteen after initial set up and the first sowing of seeds.

Plant Sampling Protocol

Eight weeks into the trial being conducted there were multiple pieces of data gathered. Spatial data was gathered by calculating canopy coverage for each species. This was done by taking a percent canopy coverage of grasses and forbs in each pot, adding up to 100%. This was all done before the spotted knapweed invasion was conducted.

At week 16 the height of the same 3 individuals of each species in each pot was measured. Spatial data was also gathered for each pot by calculating canopy coverage of each species, adding to 100%. Then the seedlings were clipped at soil level, sorted by species, and dried to be weighed and analyzed. The root mass from each pot was also harvested and dried to weigh and analyze.

Soil Sampling Protocol

A soil sample was taken from each pot at the end of the trial (week 16) after homogenizing the soil in each pot.

Soil pH was analyzed using non-sieved samples from each of the pots. To prepare the samples 5 grams of unsieved soil was mixed with 5 mL of deionized water. The sample was then homogenized and centrifuged for five minutes at 5000 rpm. The samples were allowed to settle for 24 hours before using (pH measuring instrument) to measure the pH for all 144 samples.

Soil was prepped for analysis by sieving soils with a 2 mm fine mesh sieve and then dried in a Yamato drying oven (model DKN812) at 80°C for 12 hours to remove moisture.

Once dried, each sample was ground to a fine powder using a mortar and pestle to prepare for the furnace oven. Once ground, 4-5g of each sample were placed in small ceramic crucibles and placed in the furnace to burn at 500°C for 5 hours. They were then weighed again to calculate the percent organic matter for each sample.

The dried and ground soils were also analyzed for total carbon, nitrogen, hydrogen, and sulphur using Thermo Scientific FlashSmart CHNS/CHNS elemental analyzer. 10-15 mgs of soil were weighed and placed into small tin capsules and placed into the elemental analyzer wheel for analysis. The values were generated as a percent value of the total sample.

DATA ANALYSIS

Although I expected to analyze the priority effects of native species versus invasion, there was limited growth from our exotic species, spotted knapweed (*Centaurea stoebe*). For this reason, I excluded that factor from analysis.

Priority Effects Analysis

Priority effects were calculated using the priority strength calculation first described in Vanette and Fukami (2014) and later adjusted in Sarneel (2016). Aboveground biomass, separated out by individual species, collected after 16 weeks of growth was used to calculate priority. After the samples were separated by species, they were placed in paper bags and dried at 65°C for 48 hours in a drying oven (Yamato DKN812 drying oven) and weighed to determine total sample weight after drying.

The strength of priority effects was calculated by using the natural logarithm of the ratio of species percent cover (D) of species (i+1) when it was sown after species j and before species j (Equation 3.1).

Equation 3.1

$$\text{Priority strength} = \ln(d(i_{ji})/d(i_{ij}))$$

Where the subscript will show the planting order of the two species. A positive priority strength value will depict facilitation and a negative value will depict inhibition. This test allows us to directly quantify and compare the priority strength of species sown when planted first or second in the field.

Two-factor analysis of variance (ANOVA) were performed for both plant groups (ES and LS) and each unique species seeded priority value to compare the effect of the three seeding treatments, and the two fertilization levels.

Flora Diversity Analysis

Plant cover data from each pot was compared using Shannon diversity indices, as well as species richness. In addition, a two-way ANOVA was performed for exotic coverage at each plot to compare the effect of the two fertilizer levels, and the three seeding treatments.

Root biomass data from each pot was compared against the three seeding treatments and two fertilizer levels using a two-way ANOVA.

Soil Analysis

A two-way ANOVA was performed for soil pH, and each individual soil element (carbon, nitrogen, hydrogen, and sulphur) to compare the effect of the three seeding treatments and the two fertilizer levels.

All analyses were run in R, version 4.0.5. A Q-Q plot was created for each ANOVA to check for normality, and a F-test was run for each ANOVA to check for variance.

RESULTS

Priority Effects Results

The mean priority values for each species in each pot, regardless of treatments received, was evaluated. LS species (showy milkweed and fescue Spp.) showed a significantly weaker priority value compared to all the ES species (yarrow, slender wheatgrass, Sandberg's bluegrass, and blanketflower) ($F_{5,115} = 30.66$, $p < 0.001$) (Figure 3.5). Showing that the ES species are less determenant on arrival, showing similar growth whether planted first or second. While the LS species have a significantly higher amount of growth when they are planted first.

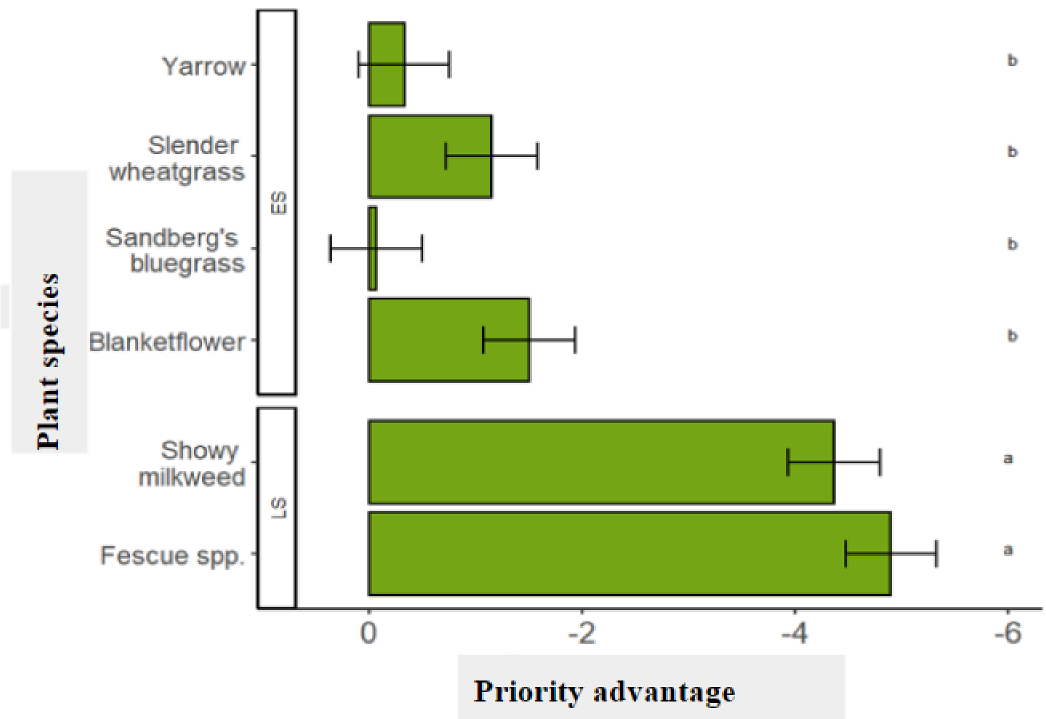

Figure 3.5: Priority advantage observed for each plant species sown (± SE). A negative priority advantage indicates inhibition of growth when planted second, a positive priority advantage indicates facilitation of growth when planted second. Differences in letters above individual bars indicate significance groupings.

Differing fertilizer levels did not affect the priority of plants in those pots ($F_{1,115} = 1.09$, $p = 0.296$) (Figure 3.6).

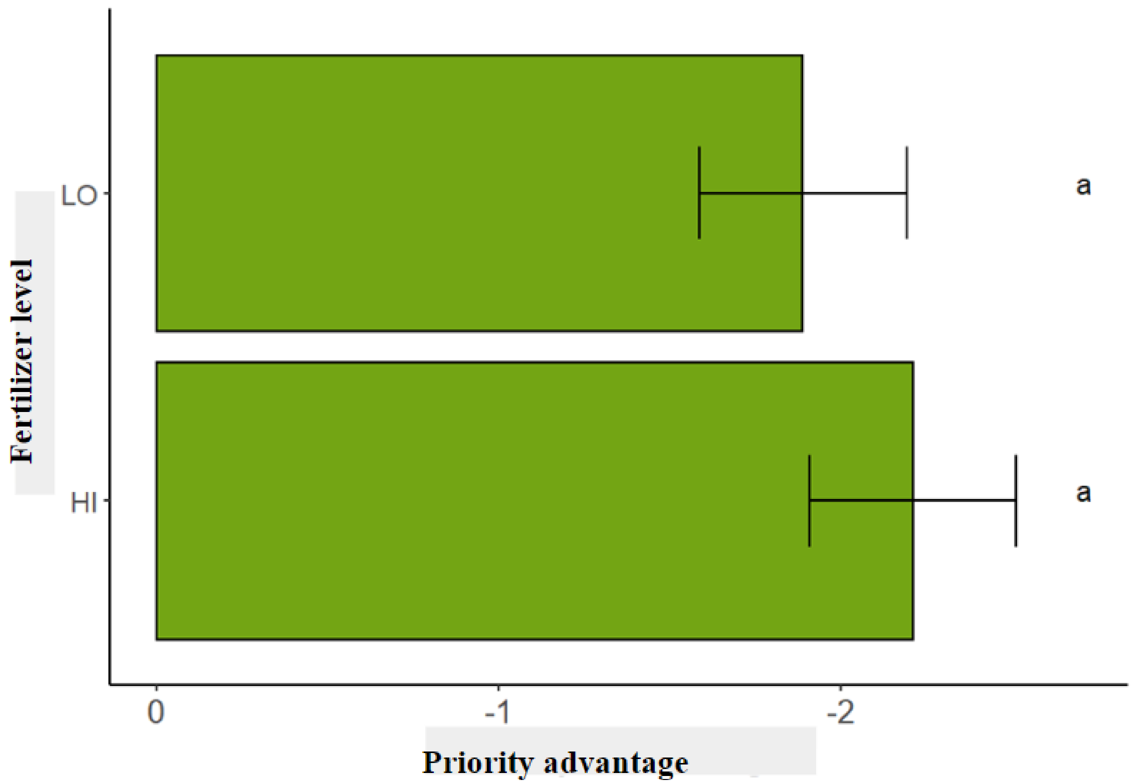

Figure 3.6: Priority advantage based on fertilizer treatments for each pot (± SE). A negative priority advantage indicates inhibition of growth when planted second, a positive priority advantage indicates facilitation of growth when planted second. Differences in letters above individual bars indicate significance groupings.

Flora Diversity and Biomass Results

The relative biomass of each species compared to itself, separated by seeding order the pot received, showed that seeding order in some cases influenced relative biomass a species produced. Slender wheatgrass and fescue Spp. showed an increase in relative biomass when planted first. No difference in relative biomass was witnessed for all other species, whether seeded first or second ($F_{5,264} = 99.69$, $p < 0.001$) (Figure 3.7).

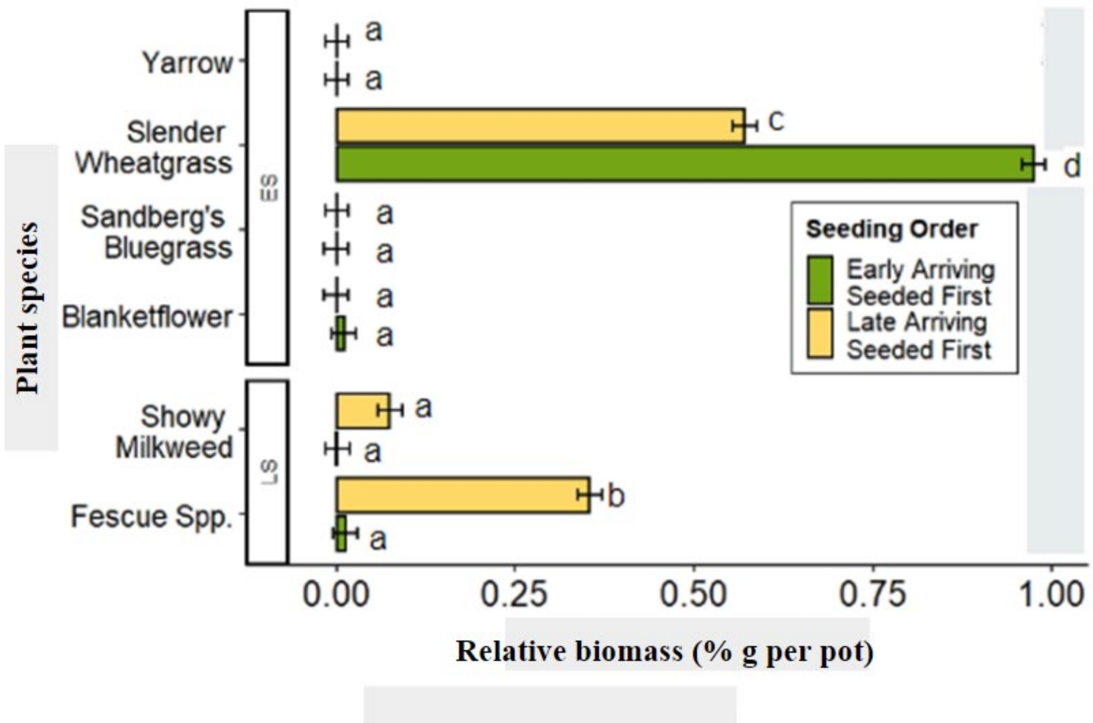

Figure 3.7: Relative biomass of each plant species, separated out by planting group, versus seeding treatment (± SE). Differences in letters above individual bars indicate significance groupings within unique species.

The relative biomass of each species compared to itself, separated by fertilizer level the pot received. There was no difference in each individual species relative biomass when compared to the fertilizer level a pot had received ($F_{5,264} = 0.483$, $p = 0.79$) (Figure 3.8).

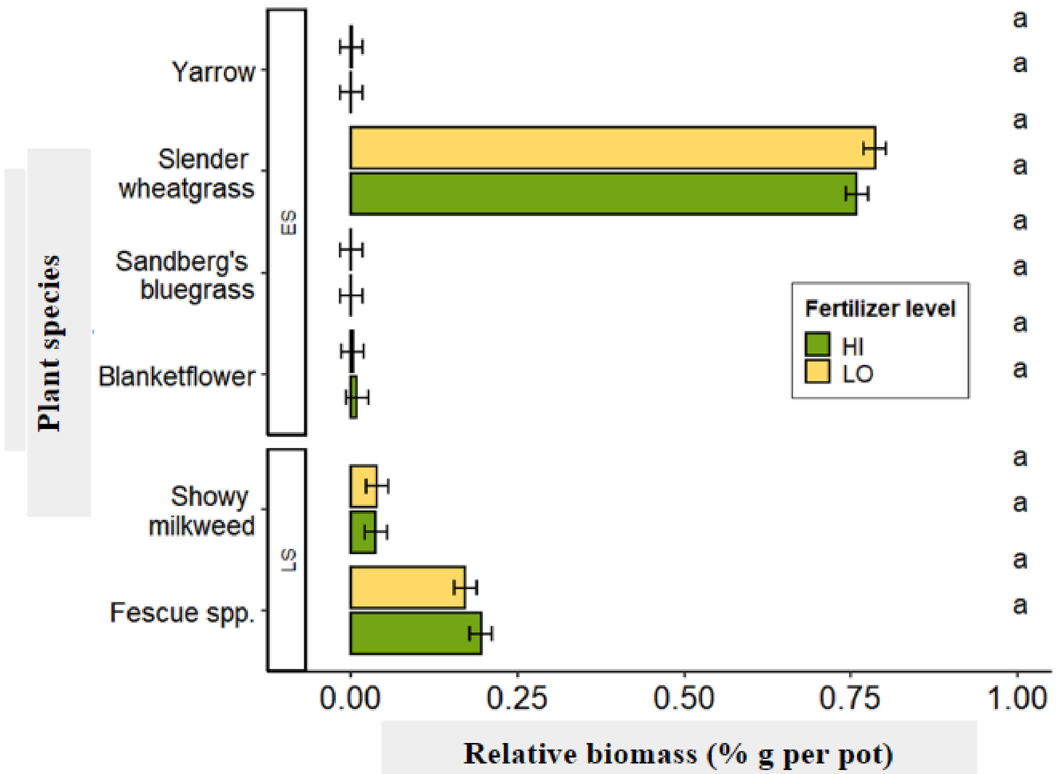

Figure 3.8: Relative biomass for each plant species, separated by planting group, versus fertilizer level (± SE). Differences in letters above individual bars indicate significance groupings within unique species. Note that there is no significant difference shown by any species when relative biomass is compared to fertilizer level a pot received.

Pots that received the LS seeding treatment had a significantly lower root biomass than pots that received either the ES or ESLS seeding treatments ($F_{2,61} = 13.07$, $p < 0.001$) (Figure 3.9).

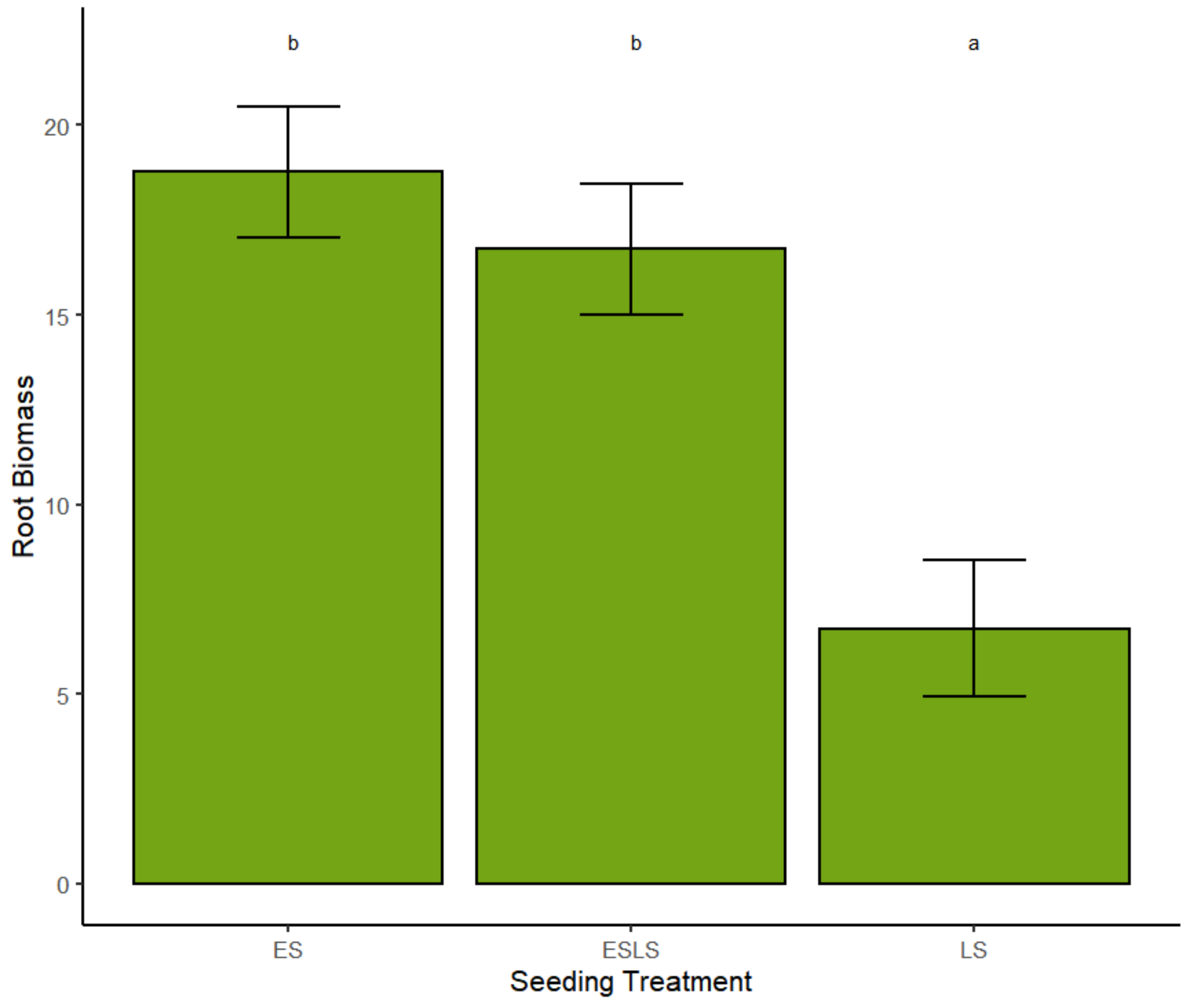

Figure 3.9: Mean root biomass weights compared against seeding treatment received (± SE).

Shannon diversity was calculated for each pot, then compared by the fertilizer level that each pot received. Pots that received the low fertilizer treatment had a higher diversity than the pots that received a high fertilizer treatment ($F_{1,66} = 15.49$, $p < 0.001$) (Figure 3.10).

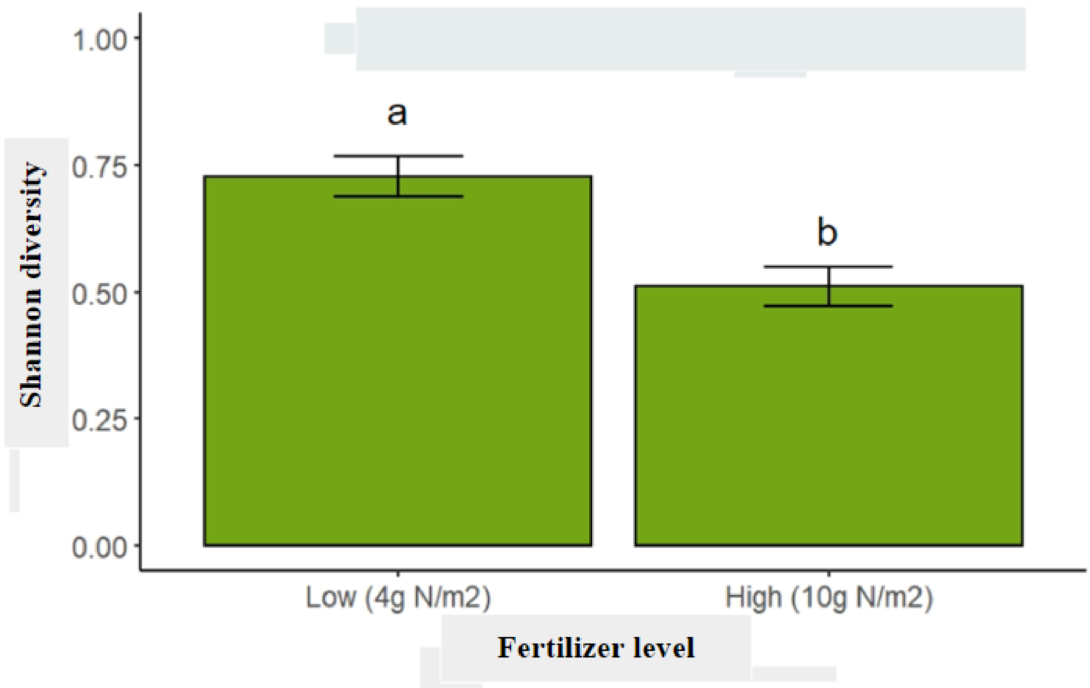

Figure 3.10: Shannon diversity in each pot versus fertilizer level the pot received (± SE). Differences in letters above individual bars indicate significance groupings.

The mean Shannon diversity in each pot was different when compared to the seeding treatment each pot had received. LS pots showed the highest diversity when compared to my other two seeding treatments, while ES had the lowest diversity of the three treatments. Diversity in pots that received an ESLS seeding treatment had the second highest diversity ($F_{2,66} = 39.64$, $p < 0.001$) (Figure 3.11).

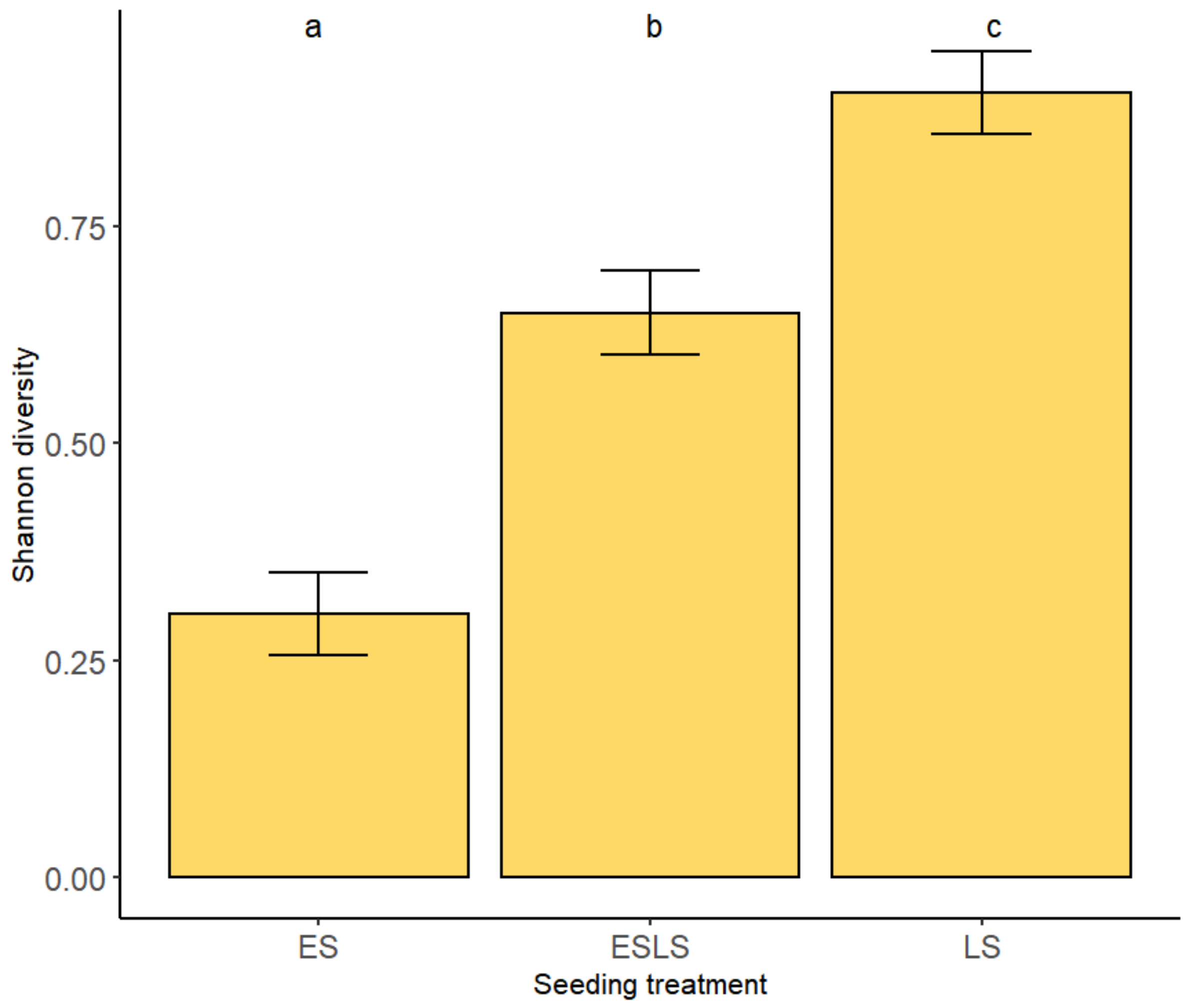

Figure 3.11: Shannon diversity in each pot versus the seeding treatment the pot received (± SE). Differences in letters above individual bars indicate significance groupings.

Soil Analysis Results

Pots that received the low fertilizer level treatment had a significantly higher pH than plots that received the high fertilizer level treatment ($F_{1,66} = 16.88$, $p < 0.001$) (Table 3.3). There was no significant effect of the seeding treatments each pot received on the soil pH in each pot ($F_{2,66} = 0.66$, $p = 0.517$) (Table 3.3).

Table 3.3: Mean soil pH when compared across fertilizer levels and seeding treatments.

Fertilizer Level	Mean Soil pH	Group
High	6.28	a
Low	6.52	b

Seeding Treatment	Mean Soil pH	Group
ES	6.47	a
LS	6.52	a
ESLS	6.45	a

DISCUSSION

Planting order had a significant effect on the total biomass production of both ES and LS plant species. LS species had a more negative priority value compared to ES species, meaning that LS species grew more predominantly when planted first than second, while ES species as a group had a similar amount of growth whether they were sown first or second. Diversity was affected by both the fertilizer level a pot received, pots receiving a low fertilizer treatment had a higher amount of diversity, and the seeding treatment a pot received. The pots that received LS species first had higher levels of diversity compared to the pots receiving the ES species first, which had the lowest level of diversity.

Priority Effects and the Effects on Relative Biomass

Priority effects, in our case, were not significantly affected by fertilizer levels (figure 3.6). They were affected by arrival order depending on the successional status of the plant (figure 3.5). Late successional species grew significantly more when planted first, while most early successional species showed similar growth whether planted first or second (figure 3.5). Relative biomass for fescue spp. and slender wheatgrass both increased when they were planted first (figure 3.7).

The late successional seeding group had a more negative priority value when compared to the early successional seeding group, meaning that they gain an advantage in establishment and growth when planted first rather than second. This is the opposite for the early successional seeding group which emitted a priority value closer to zero for all four species. The strongest priority value is shown by Sandberg's bluegrass, then yarrow, then slender wheatgrass, and then blanketflower with the weakest priority value, showing that early successional species can grow well whether they are seeded first or second. Prior research has shown the same results, with early successional plants emitting stronger priority effects, especially in newly colonized ecosystems (Erikkson and Erikkson 1998, Kleijn 2003, Sarneel 2016, Yu et al. 2020).

A greater amount of relative biomass was produced for late successional plants as a whole planting group when planted first. When broken down by individual species only fescue spp. had a significantly higher relative biomass when planted first versus second. Analyzing data on the early successional species showed all four species had a similar growth when planted first or second.

These results are expected, as early successional plants tend to be able to grow quicker, and sequester nutrients, space, and light with more ease than late successional plants. The quick growth and establishment in a new ecosystem allow early successional plants to crowd out and outcompete plants arriving or establishing themselves later, allowing them to have a more positive priority value, having considerable amounts of growth whether planted first or second. A trend that is further shown when looking at the relative biomass for all four early arriving species, being similar when you compare their growth between the pots they were seeded first in or second in.

As for late successional plants, they perform significantly better when planted first, which can be expected. Rough fescue has been classified as a disturbance-sensitive late successional grass (Elsinger et al. 2022), Rocky Mountain fescue has been classified as a late colonizer in grasslands (Degn 2001), Idaho fescue has been found to be late seral (Ursek et al. 2018), and showy milkweed has been found to be a mid-successional forb (Ulev 2005). When compared to the early successional species used this means that all four species take time to establish themselves in an ecosystem, especially when resources and space are significantly sequestered and limited.

One thing to note when looking at the relative biomass of the early arriving species is the significance of slender wheatgrass' coverage. It outcompetes and produces drastically more biomass than the rest of the plant samples. It has been found that slender wheatgrass is a competitive grower (a plant with rapid growth potential (Grimes 1979)) after a disturbance event, and quickly colonizes an ecosystem after a disturbance event (Bartos and Mueggler 1982, Tilley 2011).

Root Biomass

Pots that received a seeding of the early successional plants first showed a higher amount of total root biomass. This held true whether the pot was only seeded with the early successional seeds by themselves or seeded with both early and late successional seeds at week 0. Pots sown with late successional seeds first had the lowest total root biomass. This high amount of root biomass in the pots seeded with early successional plants at week 0 is thought to be due to the overwhelming growth of slender wheatgrass in those pots. However, since we were unable to separate the roots by species, I was unable to confirm the roots were primarily from slender wheatgrass.

Shannon Diversity

I predicted greater diversity in the pots that received the high fertilizer treatment. However, pots receiving the low fertilizer treatment had the highest diversity.

These results do make sense for a few reasons. Firstly, the plants sown are native to the semi-arid grasslands of the British Columbia interior which is a naturally nutrient deficient ecosystem (Schwinning and Sala 2004). Thus, the larger than normal nutrient influx from the high fertilizer treatment could have been too much for some species of plants used, or the nutrient deficient soil did not allow for the plants arriving first to crowd the pot before the plants that arrived second were seeded. The higher fertilizer could have also made the soil unhealthy for some species seeded, and it has been suggested that healthy soil will have an increase in plant diversity, plant growth, and plant nutrient uptake (Kirankumar et al. 2008, Cummings 2009, Guinazu et al. 2009). Another reason I could have witnessed these results is because the high fertilizer levels provided our quickest growing plant, slender wheatgrass, so many nutrients that it quickly outgrew and crowded out other species that were seeded.

I also examined the effect of planting orders on Shannon diversity. Figure 3.10 shows a gradual increase in diversity as the late successional species are given more time to grow and less competition. The highest diversity was in the pots seeded with late successional species first, while the pots with the least diversity were seeded with early successional species first. The pots seeded with both sets of seed at week 0 had a Shannon diversity that landed between these two.

The observed diversity results were expected, and previous research shows consistency with my results. Delory et al. (2019) found that the ordering of community assembly has a significant effect on net biodiversity, and Weidlich et al. (2017) found that the arrival order of plant functional groups affects the diversity in an ecosystem up to three years later.

Late successional species have a tougher time establishing in recently disturbed sites, while early successional species can establish quickly, and competitively (Kleijn 2003). The late successional species are slower to sequester nutrients and establish in an ecosystem and are not considered as strong competitors as the early arriving species (Kleijn 2003). Research has shown that intervention, particularly with soil amendments and inoculations, is needed to help establish a late successional grassland community, post disturbance (Kardol et al. 2007, Kulmatiski et al. 2008, Torok et al. 2011, Middleton 2012, Koziol and Bever 2017). Thus, giving the late successional species more time to sequester nutrients from the soil and space to colonize, as well as providing assistive intervention, may give late successional species the chance to compete with the early arriving species once they are seeded.

Effects of Fertilizer Levels

Beyond the effects of differing fertilizer levels on Shannon diversity, there were no significant differences due to differing fertilizer levels in priority effects, relative biomass, or root biomass. This contradicts many findings regarding the effects of fertilizer. Rajaniemi (2008) found that fertilizer decreased species diversity. Jarchow and Liebman (2012) found that fertilization may create stronger priority effects for certain plants and less diverse ecosystems. Using fertilizer has also been found to increase both aboveground biomass (LeBauer and Treseder 2008, Jarchow and Liebman 2012). While belowground biomass is more variable in its response to fertilization, showing an increase in root growth with an increase of P, while increases in N depended on the nitrogen turnover of the soils the plants are growing in (Keller et al. 2022).

Even though the nutrient levels in the pots treated with the high fertilizer treatment were significantly greater than the pots treated with the low fertilizer treatment (Appendix F), I expected a bigger nitrogen difference. One reason there may not have been such a difference is due to the use of a slow releasing fertilizer. The slow releasing fertilizer was applied as small pellets of fertilizer that would leach into the soil overtime. Although the suggested leaching time stated by the product used was four months, at the conclusion of the study I observed some of these pellets still filled with some fertilizer, showing that not all the fertilizer applied had been made available to the plants throughout the experiment (Scotts Osmocote Smart-Release Plant Fertilizer, 15-9-12 Formula Information Page). I suspect that the different variables' response to fertilizer would be significant if all the fertilizer leached out.

My research showed the benefits of prioritizing seed arrival on total productivity and species diversity in an ecosystem. If the restoration goal is quick coverage after a disturbance then seeding ES species first will be recommended. If the restoration goal is to promote and maintain a diverse native ecosystem after a disturbance then seeding LS species first would be most successful.

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CHAPTER 4: CONCLUSION

SUGGESTIONS FOR RESTORATION

As humanity continues to grow, the need for infrastructure projects, resource extraction, and other anthropogenic caused disturbances will continue to grow as well. Reclaiming and restoring disturbed ecosystems will become of the utmost importance. My research has provided insight into another tool, priority effects, which can be utilized in restoration efforts in the grasslands of the interior of British Columbia.

Usage of priority effects in the greenhouse and the field showed varying effects. In the greenhouse it was clear that the establishment of late successional plants prior to the arrival of early successional plants or exotics allowed for more species diversity and richness. While the early establishment of early successional plants allowed for more root biomass and aboveground biomass. My research was unable to compare seeding orders in the greenhouse to the invasion of exotics due to the unsubstantial germination of our exotic species, spotted knapweed. Research does suggest that the early establishment of native species will allow for the reduction of exotic germination and establishment, while increasing native diversity (Abraham et al. 2008, Stevens and Fehmi 2011, Dickson et al. 2012). Results in the field were characterized by site specific responses by both the early and late successional species. Overall, late successional species had a more positive priority value, contradicting the findings from the greenhouse study. I speculate the difference in results is due to unknown biotic or abiotic factors occurring in the field, specific facultative responses, or the establishment of voluntary species arriving during the length of the experiment. However, there was no effect on exotic coverage between different seeding treatments or amendment treatments.

The greenhouse and field results show that. Further research is needed to test priority effects and benefits in deterring exotic growth as previous evidence has found benefits in utilizing priority effects to limit exotic establishment (Mwangi et al. 2007, Dickson et al. 2012, Yu et al. 2020). The priority value of native plants is site dependent, showing the importance of local knowledge for restoration success and the most optimal usage of priority effects.

The utilization of amendments in the field showed varied results. Straw matting had no significant difference in soil characteristics versus the control plots but allowed for a decrease in overall plant establishment. However, this must be viewed as a negative as exotic coverage did not significantly change versus the control plots. There was also no significantly different soil characteristics in plots receiving biochar versus the control plots. This contradicts previous research done suggesting that biochar increased soil moisture and organic matter (Wardle et al. 2008, Jeffery et al, 2011, Novak et al. 2012, Basso et al. 2013, Masiello et al. 2015, Haider et al. 2017). However, many stated benefits of biochar were not measured in this study including carbon sequestration (Lal 2008, Sohi et al. 2010), increased soil structure (Cao et al. 2009, Chen and Chen 2009), and an increase of soil microbial biomass and enzymatic activities (Smith et al. 2010, Jones et al. 2011, Lehmann et al. 2011). Lastly, plots treated with both the biochar and straw matting amendments showed a significant increase in soil moisture.

The implications of our study into soil amendments show that the usage of both biochar and straw matting may be best for both long-term and short-term restoration practices in the grassland of the interior of British Columbia.

RESEARCH LIMITATIONS

Due to Covid related logistical difficulties and extreme wildfires around British Columbia in recent years, procurement of seeds was strained. The difficulties of seed procurement laid in finding copious quantities of native late successional forbs. The original research design used two forbs and grasses for both the early successional seed pack and the late successional seed pack. However, due to the difficulties of obtaining native late successional forbs seeds, my design instead used an additional native late successional grass. This way I was able to keep the seeding treatments the same between the early successional seed pack and the late successional seed packs.

My research focused on the ability of an ecosystem to respond after disturbance with the help of priority effects and amendments. The disturbance that took place was completely manual, which was sufficient in this case. However, my manual disturbance was unable to churn the soil at any depth and only caused disturbance to the top layer of the soil. In many construction projects this would not be the case as the topsoil would be stripped and placed aside to be used again after the project completion.

The time needed for many restoration projects is well documented in literature as 3-6 years (Stromberg et al. 2007, Hedberg and Kotowski 2010, Rehounkova et al. 2021). Due to industrial partner's and master projects timelines this research was conducted over 2 growing seasons. Time limitation is a reason for the greenhouse portion of this project, allowing me to dive into specific mechanisms of native grasses and forbs priority interactions within a controlled environment. Future research needs to be focused on a longer time scale to look at the long-term effects that priority effects may have on community structure after disturbance.

CONSIDERATIONS FOR FUTURE RESEARCH

Considerations for future research should focus on implementing large-scale long-term experimental settings of priority effects. Allowing researchers to look at how a community develops over time, and how different planting orders affect the community establishment over that time scale. My research showed significant response differences based on site location, showing the importance of local knowledge on the effectiveness of priority effects. For this reason, any future projects should focus on how site specificity affects priority of native species, as well as continued testing of priority effects in a wide variety of ecosystem types. Finally, the continued testing of different amendments to assess the benefits in establishing a native community after disturbance.

This study shows that the use of priority effects and amendments in a restoration setting is beneficial to establishment of a native community, while also showing potential in deterring exotic species. Priority effects and amendments have many potential uses in helping to restore and reclaim land after anthropogenic disturbances.

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APPENDIXES

APPENDIX A: Germination Trials

To find the germination percentage of each species a germination trial was set up. Four petri dishes with filter paper were set up for each species with 20 seeds of the corresponding species seed on each petri dish. The trial was run for three weeks, and each petri dish was watered twice a week to wet the filter paper. The sprouted seedlings for each species were counted and used to calculate a germination percentage. The germination percentage was then used to calculate the number of seeds the plots or pots needed to receive to have the "viable" seed count necessary. In the end the viable seed count for the field was 100 seeds at each plot and for the greenhouse was 35 seeds for each pot.

Table A.1: The germination percent, field seed count and greenhouse seed count for the 11 unique species used throughout this study.

Plant	Germination %	Field Seed Count (100 Viable Seeds)	Greenhouse Seed Count (35 Viable Seeds)
Western Yarrow	73.75%	136	48
Rough Fescue	30.00%	333	117
Rocky Mountain Fescue	86.25%	116	41
Idaho Fescue	72.50%	138	49
Sandberg's Bluegrass	91.25%	109	39
Slender Wheatgrass	48.75%	204	72
Blanketflower	52.30%	191	67
Arrowleaf Balsamroot	70%	143	X
Italian Annual Ryegrass	95%	105	X
Spotted Knapweed	46.67%	X	22
Showy Milkweed	72%	X	37

APPENDIX B: Kenna 2021 Baseline Soil Samples Data

Table B.1: Baseline means soil organic matter at each site.

Baseline Site	Mean % Soil OM	Group
Site 1	7.73	a
Site 2	7.77	a
Site 3	7.88	a

Table B.2: Baseline means percent soil moisture at each site.

Baseline Site	Mean % Soil Moisture	Group
Site 1	18.2	a
Site 2	13.4	b
Site 3	18	ab

Table B.3: Baseline means soil pH at each site.

Baseline Site	Mean Soil pH	Group
Site 1	6.7	a
Site 2	6.83	a
Site 3	6.82	a

APPENDIX C: Pairwise P-Value Plots

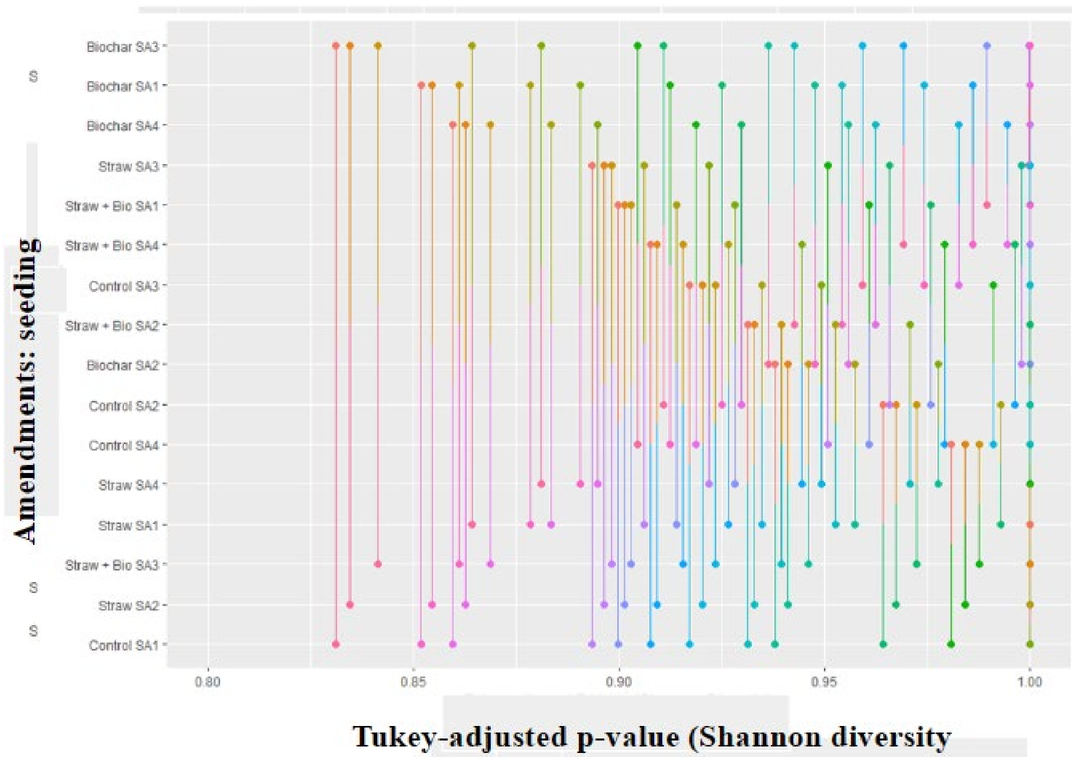

Figure C.1: Amendment and seeding combinations a plot received versus the Tukey-adjusted P value of the species richness at each plot.

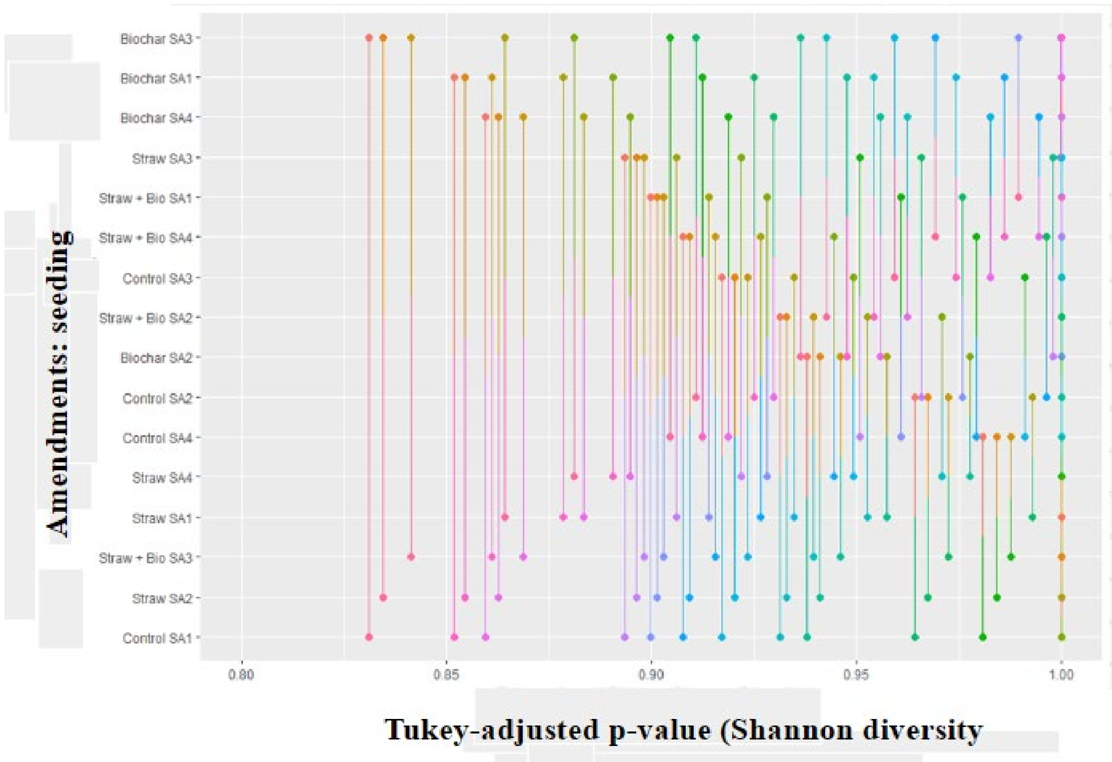

Figure C.2: Amendment and seeding combinations a plot received versus the Tukey-adjusted P value of the percent organic matter at each plot.

APPENDIX D: Field Exotics

Table D.1: Exotic species seen on field sites in Kenna Cartwright Park.

#	Scientific Name	Common Name
1	*Centaurea stoebe*	Spotted knapweed
2	*Tragopogon porrifolius*	Salsify
3	*Taraxacum spp.*	Dandelion
4	*Bromus tectorum*	Cheatgrass
5	*Verbascum thapsus*	Mullen
6	*Lactuca serriola*	Prickly lettuce
7	*Collinsia verna*	Blue-eyed Mary
8	*Descurainia sophia*	Flixweed
9	*Cirsium spp.*	Thistle

APPENDIX E: Field NDVI Maps

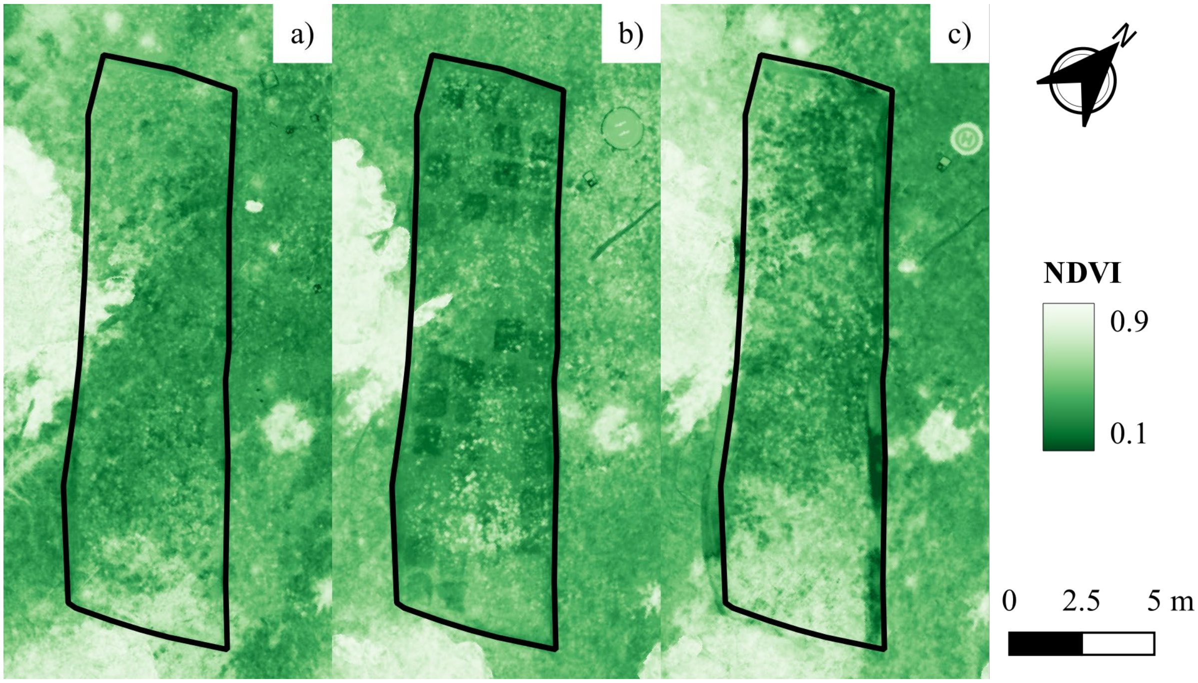

Figure E.1: NDVI maps of the upper site located in the Ponderosa Pine (PPxh2) biogeoclimatic zone. The darker the green, the less vegetation at that location. While the lighter the green up to white, the more vegetation at that location. a) Is the NDVI pre-disturbance, taken in May of 2021. b) Is the NDVI after one growing season, taken in October of 2021. c) Is the NDVI after two growing seasons taken in July of 2021.

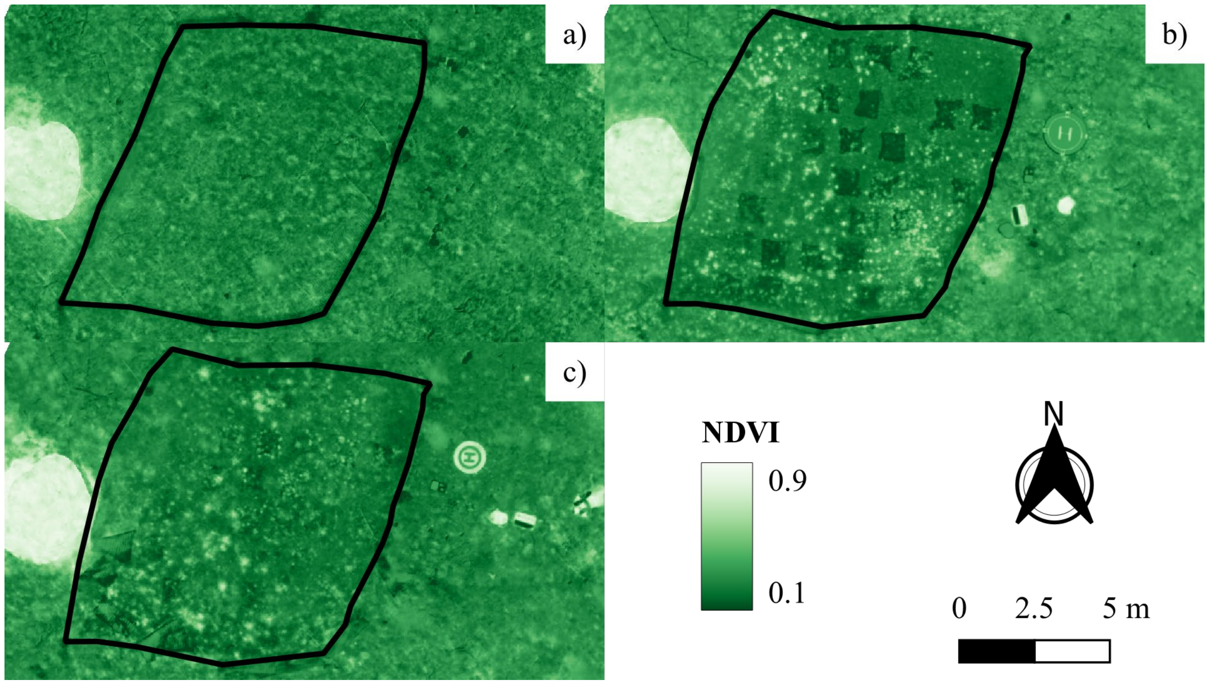

Figure E.2: NDVI maps of the middle site located on the boundary of the Ponderosa Pine (PPxh2) and Bunchgrass (BGxw1) biogeoclimatic zones. The darker the green, the less vegetation at that location. While the lighter the green up to white, the more vegetation at that location. a) Is the NDVI pre-disturbance, taken in May of 2021. b) Is the NDVI after one growing season, taken in October of 2021. c) Is the NDVI after two growing seasons taken in July of 2021.

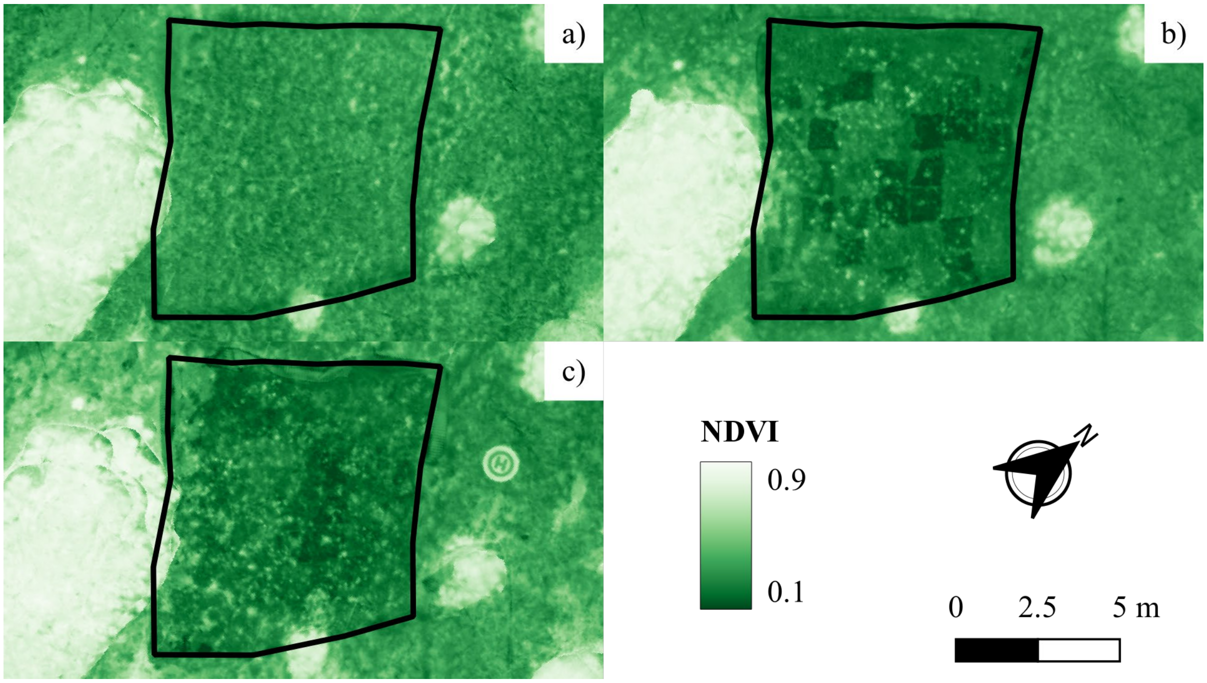

Figure E.3: NDVI maps of the lower site located in the Bunchgrass (BGxw1) biogeoclimatic zone. The darker the green, the less vegetation at that location. While the lighter the green up to white, the more vegetation at that location. a) Is the NDVI pre-disturbance, taken in May of 2021. b) Is the NDVI after one growing season, taken in October of 2021. c) Is the NDVI after two growing seasons taken in July of 2021.

APPENDIX F: Greenhouse Soil Nitrogen Results

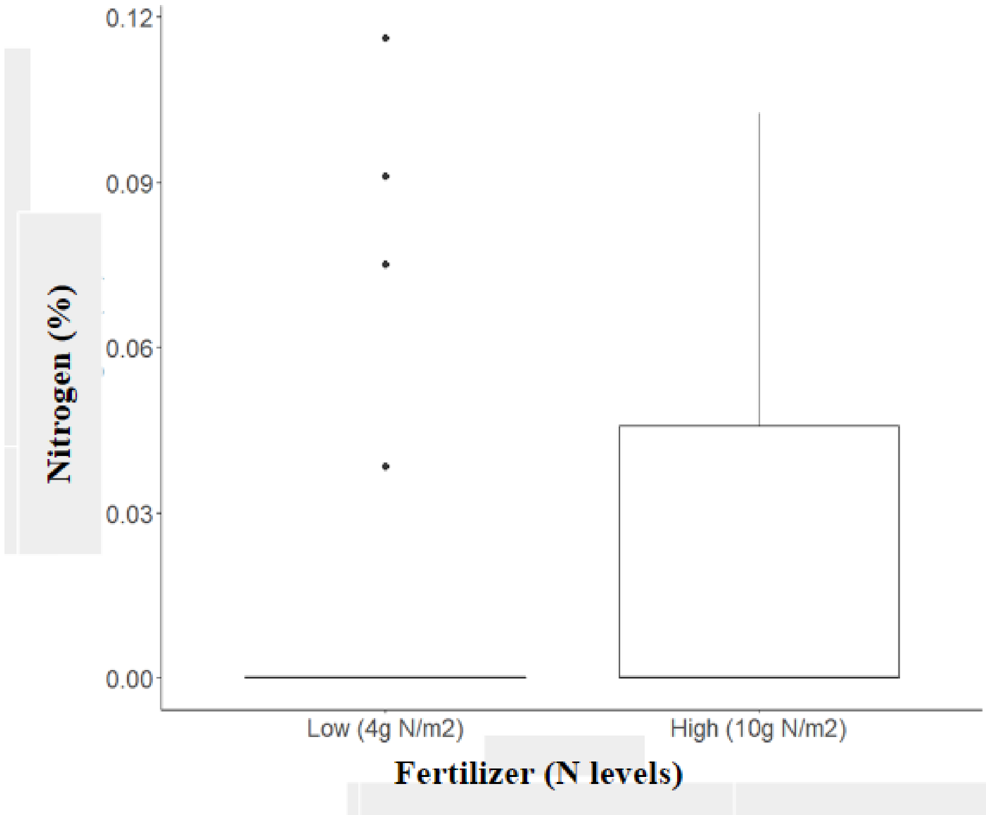

Figure F.1: Nitrogen levels in pots receiving high and low fertilizer treatments. Pots receiving the high fertilizer treatment showed significantly higher levels of nitrogen compared to pots receiving the low fertilizer treatment ($F_1 = 5.356$, $p = 0.02065$).