# EFFECTS OF ELEVATED TEMPERATURE, RAINFALL AND SOIL NUTRIENTS ON ACACIA MEARNSII INVASION



# A thesis submitted in fulfilment of the requirements for the degree of

Master of Science in Environmental Science

Department of Environmental Science Rhodes University

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# Declaration

By submitting this thesis electronically, I declare that the entirety of the work contained in this document is my own, original unaided work, that I am the author thereof and that the entirety or any part of this thesis has not been previously submitted for obtaining any qualification and will not be presented at any other University for a similar degree. All sources have been indicated and acknowledged by means of complete references accordingly.

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03 June 2021

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# Abstract

Climate change is associated with the risk of plant invasion hence a better understanding of the effects of elevated temperature, precipitation and soil nutrients on dominant invasive plants is needed for effective ecological planning. This study was set out to: (i) examine how elevated temperature  $(\pm 2^{\circ}C)$ increase), (ii) high (above local average) and low (below local average) precipitation, (iii) elevated soil nutrient content (increase in soil N), and (iv) a combination of the above manipulations affects germination and growth of Acacia mearnsii, a dominant invasive plant in South Africa. The study further evaluated how the above-mentioned treatments affect soil chemical properties following A. mearnsii germination and growth. The above-mentioned specific objectives were tested under manipulated greenhouse conditions over six experimental months. The results indicated that the above-mentioned climate change scenarios have the potential to facilitate germination and growth of the invasive species A. mearnsii, and this is likely to proliferate its invasion in future. Results showed that seed germination was significantly high under all climate change manipulation treatments (>50%) with highest seed germination recorded under high rainfall treatment (64%). Plant height was significantly higher under high temperature and high rainfall treatments throughout all the experimental months, though it was lowest under high nitrogen and combined treatment with high rainfall. The numbers of branches were high under higher temperature and low rainfall treatments than under high rainfall, high nitrogen and both combined treatments of low and high rainfall. Relative to the control, plants grown under climate change scenarios increased their root lengths, but this varied across different treatments. Total dry biomass was relatively high under high temperature treatment (0,7 g). Lower plant dry biomass was observed under low and high rainfall treatments (0,4 g)g), high nitrogen and combined treatments with both low and high rainfall treatments (0,1 g). Concerning the effects of climate change scenarios on soil chemical properties, soil pH levels were significantly higher after A. mearnsii germination and growth than before the experiment was setup. Soil resistivity was significantly higher in climate change treatments receiving nitrogen and combined treatments of low rainfall than other treatments and the soils before experiment. Soil total P was significantly higher in all the climate change treatments after A. mearnsii germination experiment than the before experiment soils. Soils receiving high temperature, high nitrogen, and combined treatment of low rainfall had significantly higher soil total N than other treatments and the before experiment soils. Soil total C was significantly higher in soils receiving high temperature, high nitrogen, and combined treatment of low rainfall after A. mearnsii germination than other treatments and before experiment soils. The findings suggest that future climate change scenarios of increased temperature and rainfall with soil nutrients could considerably enhance growth and germination success of the invasive plant A. mearnsii. Similarly, climate change scenarios could enhance some soil nutrient properties, which in turn, is likely to give the invasive plant A. mearnsii a germination and growth advantage. These results are the first in South Africa to show that future climate changes have the

potential to facilitate *A. mearnsii* germination and growth, making it more invasive. The findings have implications for invasive plants management, especially action for managing the plant through clearing of the plant in sensitive ecosystems (e.g. riparian systems).

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 interaction between treatments and months.

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# List of abbreviations

IPPC	: Intergovernmental Panel on Climate change
DFFE	: Department of Forestry, Fisheries and the
	Environment
WfW	: Working for Water
DWEA	: Department of Water and Environmental
	Affairs
pH	: Potentiometric Hydrogen ion Concentration
SCBD	: Secretariat to the Convention on Biological
	Diversity
CEC	: Cation Exchange Capacity
M	: Meter
Cm	: Centimeter
Mm	: Millimeter
G	: Gram

#### **Chapter 1: Introduction**

#### **1.1. Theoretical background**

Forecasts of the South African climate change scenario suggest that inducing atmospheric carbon dioxide is likely to elevate temperature, rainfall, and soil nutrient content (Engelbrecht et al. 2011). Such changes are likely to have severe effects on ecosystems, and previous observations on vital plant traits such as shift in plant phenology (e.g. leafing out and flowering time) suggest that plant species are already responding to global environmental change (Arnolds et al. 2015; Hoffman et al. 2009; Hoveka et al. 2016). Global climatic average temperatures are rising and are predicted to increase further in the upcoming future decades (Intergovernmental Panel on Climate Change (IPCC), 2013). It remains uncertain whether climate change scenarios will be an advantage for invasive alien plants or native plants, although it is generally accepted that future climate change scenarios will strengthen the "enemy release theory" making invasive alien plants more invasive (Rouget et al. 2004; Smith et al. 2012). This is supported by previous research, which has shown that climate change may hinder native ecosystem recovery after disturbance, thus potentially leading to the dominance of invasive alien plants (Dukes and Mooney, 1999). Furthermore, the photosynthetic rate for most invasive alien plants is more likely to increase thus giving them a growth advantage over native plants (Jia et al. 2016; Taylor et al. 2012). Moreover, under increased photosynthetic rate, water and nutrient use in invasive alien plants will be more efficient making them more resistant to extreme growth conditions (Taylor et al. 2012).

Although a few experimental studies on the effect of climate change on native plants have been conducted in South Africa (Arnolds *et al.* 2015; Musil *et al.* 2005), studies on how invasive alien plants will respond to climate change are limited. Furthermore, no study in South Africa has looked at the interactive impacts of changes in temperature, precipitation, and soil nutrient content on invasive alien plants. Climate change scenarios are more likely to lead to changes in the spread and distribution of invasive alien plants (Parmesan, 2006). For example, changes in temperature will allow plant species to move into and successfully invade new regions (Hellmann, 2008). Invasive alien plants are naturally well suited to succeed in different environments with high resource availability; this is predicted under climate change scenarios (Milberg *et al.* 1999). Climate change will lead to future warmer temperatures and increased carbon dioxide availability (Bradley, 2009). Research has shown that some invasive alien plants show a greater response to elevated carbon dioxide than native plants (Weltzin, 2003). Furthermore, invasive alien plants have short generation times, strong seed dispersal abilities, and wide-ranging environmental tolerances, and this allows them to survive better with rapid climatological change scenarios (Brooks *et al.* 2004). Extreme weather events will also lead to elevated disturbance, and invasive alien plants normally have the potential to thrive in disturbed

environments with high light availability and fragmented native plant communities (Bradely, 2009). These effects may differ from their independent and interactive effects as well as between different invasive alien plants. For example, even though plant nutrient requirements relate to temperature changes, an increase in temperature does not necessarily mean an increase in plant growth and development, because the effects of a balance in plant nutrients vary with temperature (Sardans and Peñuelas, 2012).

There is insufficient experimental evidence about specific effects of elevated individual and integrated future manipulated climate change scenarios (temperature, rainfall, and soil nutrients) on soil ecosystems with focus on chemical properties of the soil (see Fierer et al. 2005; Kardol et al. 2010). Improving the knowledge of the current understanding of future predicted changing climate scenarios on chemical properties of the soil (soil pH and resistivity, soil nutrients concentration and basic cations) is needed so that it can aid in informing decision making and management on plant invasion impacts to prevent the loss of vital soil ecosystems and functioning (Rengel, 2011). Soil ecosystems play both direct and indirect roles on plant community productivity because plants respond individually to soil properties induced by climate change scenarios (Kardol et al. 2010). A previous study reported that elevated soil surface temperature leads to altered soil processes e.g. mineralization and decomposition induced by soil microbiological activities, but this depends on frequent soil moisture maintenance (Fierer et al. 2005). In this regard, plant communities are more likely to develop from the influence driven by climate change scenarios of increased temperature, rainfall, and soil nutrients (Lafleur et al. 2010). However, soil ecosystems are indirectly altered by climate change scenarios which also affect plant communities, for example by altering abiotic conditions, processes of the soil and soil organisms driving these processes (Kardol et al. 2010). To improve the knowledge and understanding of how climate change scenarios affect soil chemical properties under plant growth, the study investigated how soil chemical properties respond to manipulated future predicted individual and integrated climate change scenarios of elevated temperature, rainfall, and soil nutrients under greenhouse conditions. Future predicted climate change scenarios are also expected to have severe impacts on soil ecosystem due to increased temperature, rainfall, and nitrogen deposition events with varying amounts and frequencies (Gelybo et al. 2018).

In this regard, experimental studies on individual and interactive effects of future climate change need to be conducted on problematic invasive alien plants. Therefore, this greenhouse study is motivated by the need to understand the response of alien invasive plants to the predicted future climate change scenarios, and the effects of the climate change scenarios on soil chemical properties before and after invasion. The broader aim is to examine shifts in plant growth and development for invasive species, *A. mearnsii. A. mearnsii* is selected because it is a well-known problematic invasive alien plant

species causing significant negative ecological and economic effects in South Africa (Richardson *et al.* 2007). The study exposed soils, planted with the above-mentioned invasive alien plant to different artificially manipulated elevated soil temperature, rainfall, and soil nutrient content (specifically soil N) in a microcosm experimental system.

#### **1.2.** Problem statement and study motivation

This study aims to examine the effects of global climate change scenarios of elevated temperature, rainfall, and soil nutrients content on the germination and growth of invasive *A. mearnsii*. Effects of climate change scenarios on invasive alien plants are difficult to predict due to uncertainty in climate change scenarios and in understanding how invasive alien plants will respond to the predicted climate changes (Walther *et al.* 2009). The global climatic factors provide the framework for a region's climatic conditions and influence invasive alien plants distribution (Richardson *et al.* 2000). Changes in temperature and rainfall events associated with rising concentrations of carbon dioxide are altering local environmental conditions, which may disturb and inhibit indigenous plant species growth and survival (Walther *et al.* 2002). According to Sorte *et al.* (2013), this enriches non-native plants with developing opportunities for successful population growth and development. Therefore, there is a need to examine how invasive alien plants will respond to different future climatic conditions. Such studies will help in developing predictive models for the future spread of invasive alien plants and how to manage such changes.

# **1.3. Description of experiment**

The study was a greenhouse-based experiment conducted at Rhodes University, in Makhanda (formerly Grahamstown), South Africa. The passively ventilated greenhouse facility allowed air temperatures to be closely approximated to outside temperature. Soils for the greenhouse experiment were collected in November 2019 on uninvaded sites (areas that are dominated by natural vegetation) in Bathurst area (33°30'14"S and 26°49'26"E), located about 43 km outside Makhanda and 12 km inland from Port Alfred on the R67 road in the Eastern Cape Province. Vegetation in the area where soils were collected for the experiment is classified under Albany thicket biome (Mucina and Rutherford, 2006), which is dominated by dense, woody, semi-succulent and thorny plants that reach an average height of 2 - 3 m. According to Acocks (1953) and Everard (1987) thickets are relatively impenetrable, especially under unaltered conditions. The biome mainly consists of different major vegetation types, and a wide variety of plant communities, with a varying structure and plant species composition. Acocks (1953, 1988) recognized four major vegetation types currently classified as a thicket, namely Valley bushveld, Noorsveld, Spekboomveld, and False karroid broken veld. However, the current Albany thicket biome vegetation is highly transformed and demonstrate high levels of degradation (Low *et al.* 1996; Palmer *et al.* 2004). Rainfall in this region is unreliable with an average

coefficient of variation of 25 - 36% and persistent droughts are common, hence there is a 25% chance of not receiving 80% of the mean annual rainfall in any given year (Aucamp and Tainton, 1984). The area experiences high temperatures in summer (October to March) that exceeds 40°C on occasions and low temperatures with frost ranging from 0 - 64 days in the winter (April to August) season (Aucamp and Tainton, 1984). Beyond the area considered for this study recent climate change trends observed in South Africa indicated moderate temperature increases ranging from 2 to  $2.5^{\circ}$ C and reaching 3°C for the far future climate change predictions and rainfall regimes fluctuating at about ±20 mm per month over various parts of South Africa. These trends are persistent and recurrent droughts attributed to changing climate (DFFE, 2017).

#### 1.4. Research objectives and conceptual framework

This study examined the effects of future shifts in germination, growth and development of invasive *A. mearnsii* under predicted future global climate change scenarios (elevated temperature, rainfall, and soil nutrients). The effects of predicted future climate change scenarios on soil chemical properties levels following invasive *A. mearnsii* growth under greenhouse conditions before and after the experimental manipulation were also examined. The following key research questions grouped in two sections, were addressed to meet the research aims:

- (A) Seed germination and plant growth responses to future predicted climate change scenarios
  - (i) How does elevated warming (±2°C increase) affect germination and growth of invasive A. mearnsii?
  - (ii) How do high (above local average) and low (below local average) precipitation levels affect germination and growth of invasive *A. mearnsii*?
  - (iii) How does elevated soil nutrient content (increase in soil N) affect germination and growth of invasive *A. mearnsii*?
  - (iv) How does a combination of elevated warming, precipitation, and soil nutrient content interact to affect germination and growth of invasive *A. mearnsii*?
- (B) Soil chemical properties respond to future predicted climate change scenarios
  - (v) How does predicted future climate change scenarios affect soil chemical properties following invasive *A. mearnsii* growth under greenhouse conditions?

#### 1.5. Thesis outline

This thesis is comprised of five chapters that are grouped as follows:

**Chapter 1** provides the relevant theoretical background as an introduction to the research problem and outline aims and objectives of the thesis.

**Chapter 2** reviews literature regarding biological invasions in South Africa, drivers of biological invasions, theories of invasion, global climate change and invasive alien plants. The chapter also

discusses the effects of elevated temperature, rainfall, and soil nutrients content on invasive alien plants, and how *Acacia* species invasion influences changes in chemical soil properties under future predicted climate change scenarios.

**Chapter 3** explores changes in seed germination rate and plant growth of *A. mearnsii* under manipulated future predicted climate change scenarios.

**Chapter 4** quantifies the effects of manipulated future predicted climate change scenarios on soil chemical properties following the growth of invasive *A. mearnsii* under greenhouse conditions.

**Chapter 5** provides an overall synthesis of the key research conclusions of Chapters 3 and 4 and future research recommendations.

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#### **Chapter 2: Literature review**

#### 2.1. Introduction

In an increasingly globalized world, the number of invasive alien species invading native plant communities continues to rise (Van Kleunen et al. 2015). Plant invasion is one of the largest problems in South Africa, with millions of hectares of land having been invaded (Richardson and van Wilgen, 2004; Vilà et al. 2011). Invasive alien plant species can survive, spread, and reproduce unaided at rapid rates across different landscapes (Nyoka, 2003). Invasive alien species are sometimes referred to as non-native, exotic, non-indigenous, and invaders that have both severe ecological and economic effects (Lockwood et al. 2007). Although many definitions exist, invasive alien species are species that have been introduced to an area or ecosystem, can survive, reproduce, and cause harm economically and environmentally within the invaded area (Lockwood et al. 2007). According to the Convention of Biological Diversity, an invasive alien species is defined a species whose invasion and spread out of their native environment has devastating threats to biodiversity (SCBD, 2009). If the factors responsible for managing invasive alien species are either absent or weak, this results in invasive alien species diversity to flourish at an abnormal rapid rate (Wijesundara, 2010). Invasive alien plants are also known to have adverse negative effects on the invaded plant communities and ecosystems (Colautti and MacIsaac, 2004; Vila et al. 2009). Furthermore, they displace native species through changing biotic and abiotic processes. However, recent studies have shown that not all invasive alien species are considered invasive because some have no adverse effect and can be beneficial (Didham et al. 2005; van Wilgen and Richardson, 2014).

An introduced species become invasive when it becomes extremely abundant and change vegetation structure (Blackburn, 2011; Iponga *et al.* 2008) and can out-compete native plants for vital resources available such as nutrients, light, physical space, and water, results in socio-economic negative impacts (Lockwood *et al.* 2007; van Klinken *et al.* 2006). In addition, they have the potential to form dense impenetrable stands restricting access to wild animals compared to native plants (Van Klinken *et al.* 2006). Most of them are successful competitors, which allow them to quickly proliferate and expand their geographic range (Bradley *et al.* 2010; Daehler, 2003; Pyšek and Richardson, 2007; Willis *et al.* 2010). Invasive alien species co-exist with native species for a while, then gradually out-compete them by adapting to the new location before growing and increasing their population (Richardson *et al.* 2003). Invasion by invasive alien species causes severe socioecological, and economic problems globally (Davis *et al.* 2000; Di-Tomaso, 2000; Dukes and Mooney, 1999; Pimentel *et al.* 2000; Pimentel *et al.* 2001; Vitousek *et al.* 1996; Williamson, 1996). However, invasive alien plants establish new habitation through enhanced resource availability including water

and soil nutrients following both natural and human induced disturbances such as veld fire and vegetation clearing (Blumenthal, 2006; Davis *et al.* 2000; Funk and Vitousek, 2007; Hobbs and Huenneke, 1992). Furthermore, the ability of a plant species to promote continued disturbance enables it to increase and spread abroad successfully (Funk and Vitousek, 2007).

In Southern Africa, alien plants invasion has major consequences for biodiversity conservation by displacing native plants resulting in a reduction in species richness and extinction (Butchart *et al.* 2010; Vilà *et al.* 2011). Invasive alien plants are considered as one of the devastating threats to biodiversity, and ecosystem service provisioning (e.g. crop pollination) and functioning (Klein *et al.* 2007; Wilcove *et al.* 1998). Invasive alien species are most likely to have a negative impact on human well-being through their impacts on ecosystem services (Pejchar and Mooney, 2009; Shackleton *et al.* 2007; Vaz *et al.* 2017). Also, when an invasive alien species reaches its higher abundance level and dominates an ecosystem it potentially influence the performance of existing individual resident plant species and their population dynamics (Vila` and Weiner, 2004), and consequently leads to direct and indirect severe effects on plant community structure and ecosystem functioning (Levine *et al.* 2003). However, high frequency of increased temperature and rainfall events may facilitate transport of invasive alien species (Miller *et al.* 2014).

# 2.2. Drivers of biological invasion

All plant invasions begin with the successful transport of propagules from their native location to a new invaded location (Lockwood et al. 2007). Invaders have the potential to escape their natural enemies when they establish themselves in a new region (Mooney, 2005). According to Lockwood et al. (2007), these plant invasions can be transported by both natural and human means. The humanassisted invasions are recognized to be intentional and unintentional, with intentional plant invasions being associated with good records of when, where, and how it occurred. The reason for the unintentional movement of propagules is mainly known for resources, e.g. food and environmental enhancement (Lockwood et al. 2007). Disturbance, whether natural or human-induced have the potential to trigger the plant invasion process. Didham et al. (2005) suggested that the main driver for plant invasion is the growing and movement of the human population worldwide, which then requires the development of industrial and agricultural facilities to support the certain human population. This development alters and triggers land use and cover, biogeochemical cycles and elevates atmospheric carbon dioxide levels. All the above-mentioned plays a significant role in global climate change scenarios and the spread of invasive alien species around the world (Didham et al. 2005). Climate change scenarios and disturbances severely affect native plants negatively but create opportunities for invasive alien plants to successfully establish (Lockwood et al. 2007). This can occur if there is enough supply of invasive alien plants propagules that can tolerate and adapt to the induced environmental conditions after a natural or a human means disturbance has occurred (Lockwood *et al.* 2005; Williamson, 2006). Native plants are capable of co-existing and out-competing non-native plants given the right growth and development conditions (Daeler, 2003). However, the problem occurs where environmental conditions are altered, as invasive alien species have greater phenotypic plasticity, that results in more competitive growth and fecundity (Daeler, 2003).

Several studies have attempted to identify traits that make invasive alien species more invasive (Baker, 1965; Crawley *et al.* 1996). However, it seems unrealistic and challenging to have a full general list of traits that explain invasiveness for all plant species (Perrings *et al.* 1993; Williamson, 1999) due to insufficient data on plant traits crucial for successful invasion. Furthermore, adaptive traits facilitating invasive alien plants growth and spread in altered habitats include rapid germination rates and high seed production (Grotkopp *et al.* 2002; Perrings *et al.* 2005), low resource levels tolerance, and ability to flourish with enhanced resources availability (Milberg *et al.* 1999). Lavergne and Molofsky (2007) suggest that several introductions of invasive alien plants lead to increased rates of phenotypic evolution. Also, common traits of invasive alien species include rapid plant growth, reproduction, and high seed dispersal ability, capability to alter growth form to suit current environmental conditions, wide ranging environmental conditions tolerance, and prior successful invasions (Ewell *et al.* 1999).

Alien species invasion patterns result from an integration of factors that include life-history traits such as propagule production and distribution patterns, germination rates, rapid growth and survival requirements, and historical factors such as time (Flory *et al.* 2006). In addition to disturbance, propagule pressure is a crucial determinant of plant invasion success (Rouget and Richardson, 2003). Three major factors that drives the plant invasion in an environment by new plant species; include propagule pressure, invasive alien plants traits, and the invasibility of the new area (Lonsdale, 1999; Williamson, 1999). However, Huston (1994) and Davis *et al.* (2000) argued that plant invasion is facilitated by the similar basic processes that allow native plant species colonization and repeated regeneration. There are several theories developed to understand invasion success that have been described relating to ecological characteristics and mechanisms responsible for successful invasion.

#### 2.3. Theories of invasion

The enemy release theory, also known as enemy escape hypothesis, is a suggestive concept that explains the invasive alien plants success (Elton, 1958; Jeffries and Lawton, 1984; Wolfe, 2002). It predicts that the distribution, spread and abundance of invasive alien plants will increase due to the reduced impacts experienced from natural enemies when an invasive alien plant is introduced into a new ecosystem (Roy *et al.* 2011). Natural enemies are significant in managing populations, but they

have a stronger controlling effect on native plants compared to invasive alien plants in the introduced range (Roy *et al.* 2011). As a result, the population growth of non-native plants increases through two distinguished main pathways described by Colautti *et al.* (2004), the regulatory and compensatory release. Regulatory release occurs when the host has low resistance defense to invasive alien species, the enemies regulate it in its native range and the reduction leads to the change in survivorship, fecundity, and biomass parameters (Roy *et al.* 2011). Compensatory release occurs when the host is well defended and reduction in natural enemies causes slight consequence to the host population, but this leads to reallocation of available resources from defense to population growth over certain ecological time (Roy *et al.* 2011).

Resource use theory arises when the resources needed by a species are in high availability due to high supplementation rate of resources (Byers, 2000) and less interference with access resource densities by resident species (Holway, 1999). It is a mechanism in which high resource availability increases the invasibility by inducing the ability of invasive plant species to actively compete with the indigenous plants (Shea and Chesson, 2002). Soil nutrients supplementation (Kolb *et al.* 2002; Rai, 2013) and water to the soil promotes the plant invasion process to succeed (Kolb *et al.* 2002; White *et al.* 1997). Previous studies have shown that the integration of high soil nutrient content and water availability can enhance the ability of invasive alien plants to out-compete the indigenous plants (Blumenthal, 2006; Kolb *et al.* 2002). However, global climate change influences the plant food resources (Krockenberger *et al.* 2012).

The concept of niche opportunity theory defines the conditions that promote plant invasion in terms of resource availability, natural enemies, physical space, the interaction between the factors and the way they differ in certain space and time (Rai, 2013; Shea and Chesson, 2002). It combines both resources, and natural enemies' theories with the physical environment contributing to an invaders growth rate (Davies *et al.* 2000). Environmental fluctuations in time and space have major effects. Therefore, an invader will be at an advantage if it can tolerate environmental harshness (Jefferies, 2000). The theory predicts that low niche opportunities resistance results from high plant species diversity. Global climate change can influence the plant species with small distribution ranges to change their distribution patterns for an adaptable better habitat (Hellmann *et al.* 2008). Furthermore, increasing temperatures can lead to drought conditions thus degrading suitability for species, which results in range shifts of plant species in diverse ecosystem (Parmesan, 2003).

# 2.4. Global climate change scenarios and invasive species

The Intergovernmental Panel on Climate Change (IPCC, 2007) defines climate change as any alteration in a region climate over a certain time, whether induced by natural or human activity. The

report published by IPCC (2007), indicated that average temperature around the world will increase with a range between 1.1 to 6.4°C by 2090 to 2099, in comparison with 1.8 to 4.0°C increase recorded between 1980 to 1999 Climate change factors including precipitation, temperature and carbon dioxide concentration have potential influence on both plant growth and soil properties (Larcher, 2003). In addition, climate change scenarios can determine the type of plants that can grow and develop at a certain region based on temperature and precipitation quantity (Banwart, 2011; Bauer et al. 1996). Climate change scenarios exerts a dominant control on the natural distribution of plant species and biodiversity (Pearson et al. 2003; Schroter et al. 2005; Vitousek, 1994), as well as the risk of plant species extinction (Sala et al. 2000; Thomas et al. 2004). Previous studies have discovered that climate change scenarios are expected to induce major threats at high latitudes regions (Sala et al. 2000). Furthermore, Parry et al. (2007) revealed that observational evidence from all continents globally shows that many natural systems are being influenced by regional climate change scenarios, mostly elevated temperatures. It is important to examine and observe how different plant species respond to both experimentally manipulated extreme warming and rainfall since it is crucial for a more up to date complete understanding of the results of effects of climate change scenarios (Cowles et al. 2018).

According to Witkowski (2002) biological invasions are a consequence of environmental changes worldwide. Walther et al. (2002) predict that global climate warming and other climatic change scenarios would affect the growth trends, phenology, and geographical distribution patterns of invasive alien plants. Dukes and Mooney (1999) and Weltzin et al. (2003) proposed that most aspects of global climate change, more especially the interactive effects between increasing carbon dioxide and temperatures, would favor invasive alien plants than native plants. Vigorous growth rates are common traits of many invasive alien plants (Simons, 2003; Willis and Blossey, 1999). Moreover, positive response to elevated carbon dioxide that induces temperatures will be expected to have severe impacts on plant life cycle (Banwart, 2011). Global climate warming affects invasive alien plants through their varied biological and ecological aspects (Richardson et al. 2000). However, invasive alien species replace native species when they are stressed and eliminated by climate change, thus climate change turns to favor invasive alien species (Cox, 2004; Dukes and Mooney, 1999; Zaveleta and Royval, 2002). According to Sutherst et al. (2007), the traits of plant species that makes them to be invasive helps them to succeed under climate change scenarios. Dukes and Mooney (1999) revealed that climate change scenarios are expected to worsen the world's invasive alien plants problems because ecosystems are more vulnerable to biological invasions when they are disturbed (Hobbs, 1991; Hobbs and Huenneke, 1992). In extreme cases across the warming world, invasions driven by climate change could most likely lead to transformed ecosystems where invasive alien

plants will have the potential to dominate consequently reducing native plants diversity (Gritti *et al.* 2006; Mack *et al.* 2000).

Climate change scenarios and plant invasion interaction have received less attention so far. Invasive alien plants are a worldwide problem that transforms various ecosystems that they invade leading to greatest impacts on important ecosystem services and biodiversity (Ortega et al. 2005; Richardson et al. 2000; Pyšek and Richardson, 2010; Vitousek et al. 1997). To reduce these impacts, it is necessary to understand the complex interaction between invasive alien plants and climate change scenarios and observe their outcomes (Grigulis et al. 2005; Myers et al. 2004). Varied climates give rise to invasive alien plants species richness and abundance (Marambe et al. 2009). For example, climate change scenarios and other environmental factors gives rise to the abnormal increase of invasive alien plants diversity and makes them to show aggressive traits (Wijesundara, 2010). Invasive alien species behavior induced by climate change scenarios gives them the capability of causing deleterious impacts on native plants diversity (Czech and Krausman, 1997). In addition, Even Charles S. Elton's classic book "The Ecology of Invasions by Animals and Plants" (Elton, 1958), recommended as the origin of Invasion Biology, warns about the invasions of native ecosystems by invasive alien species. High chances of plant invasion are induced by the key climate change scenarios for example, rainfall, temperature, carbon dioxide concentration and the soil nutrient availability. Scientists around the world have reported that climate change scenarios influence the destination habitat, and this influences plant invasion vulnerability because of lack of available crucial resources and then competition for resources take place for survival (Marambe et al. 2009). For example, warmer air temperatures and water have the potential to facilitate the translocation of species long pathways of spread that are inaccessible such as human and natural means (Marambe et al. 2009). The integration of climate change scenarios and invasive alien plants can pose devastating threats to native plant communities (Marambe et al. 2009).

# 2.5. Effects of increased temperatures on invasive plants

Plant species respond differently to extreme temperatures resulting from climate change scenarios around the globe, depending on their crucial ecological and physiological traits (Carlson *et al.* 2008). Also, temperature is amongst the essential primary factors that affects the rate of plant productivity (Hatfield *et al.* 2015). For example, some previous studies have found that plant productivity response to experimental warming is dependent on the amount of soil water content available but in a consistent manner (Elmendorf *et al.* 2011, 2012; Wu *et al.* 2011). Elevated temperature induces changes in plant community's biomass allocation and morphology (Parmesan and Yohe, 2003). Extreme soil temperature promotes plant root growth resulting from increasing metabolic activity of plant root characteristics such as root cells and lateral roots development (Repo *et al.* 2004). Contrary

to that, low soil surface temperature has the potential to limit soil concentrations and because of that plant root growth decreases (Lahti *et al.* 2002). Furthermore, as a result plant growth is directly driven by biomass allocation between aboveground plant parts (leaves, stems), and other vital plant parts (Reich, 1998). However, these elevated temperatures restrict plant physiological activity throughout summer drought season (Castro-Díez and Montserrat-Martí, 1998; Cowling *et al.* 2005; Mitrakos, 1980; Sánchez-Gómez *et al.* 2006). In addition, elevated warming facilitates plant productivity through positive effects of eco-physiological processes including resource uptake, utilization, and photosynthetic rate (Llorens *et al.* 2005). Furthermore, plant growth under extreme warming also depends on the stimulated nutrient content availability (Rustad *et al.* 2001). Alternatively, extreme warming could restrict and hinder growth of plants via induced heat stress (White *et al.* 2000). Under other conditions, warming can indirectly limit plant growth through moisture deficiency because of induced evapotranspiration (De Boeck *et al.* 2008).

Plant phenology response to extreme warming has the potential to cause changes amongst plant interactions (Brooker, 2006), consequently leading to change in composition of plant communities (Llorens *et al.* 2004). Traits that contribute to plant invasibility including wide ranging environmental tolerance and facilitated plant growth rates (Saxton *et al.* 2002), that may however favor invasive alien plants than native plants as warming increases (Hulme, 2009). Increased temperature destroys photochemical and dark reaction of photosynthesis, the photosynthetic component is most vulnerable to suffer irreversible severe damages (Baker, 1991; Havaux, 1993; Qiu and Lu, 2003). However, the damages have an impact on carbon procuring at both short and long-term reducing plant community competition and survival (Berry and Björkman, 1980; Knight and Ackerly, 2003; Reich and Oleksyn, 2004). Elevated temperatures caused by increasing atmospheric carbon dioxide may make more resources available to plants, by defrosting frozen soil and by changing rates of nutrient cycling, thus allowing plants to grow faster than they would otherwise (Weltzin *et al.* 2003). Hatfield *et al.* (2015) study found that effect of temperature on plant growth and development is mostly dependent upon specific plant species. Besides, invasive alien plants responding to increased temperature and rainfall is also a major factor that play a role in the invasion success.

#### 2.6. Invasive plants response to increased rainfall

The predictions by IPCC (2013) have showed that changes in rainfall events are expected to be less constant thus unpredictable. However, rainfall intensity and patterns are observed taking place around the globe (IPCC, 2013; Knapp *et al.* 2008). According to Volder *et al.* (2013), increasingly large fluctuations in soil moisture content following the redistribution of rainfall events drives the distribution, plant community and physiological responses of plant functional types. Further,

Elmendorf *et al.* (2011) reported that plant diversity and community structure response to elevated warming differs across a variation in ambient soil moisture. Elevated rainfall influences plant water relations by accelerating the rate of spread of some invasive alien species with excess moisture they receive (Hellmann *et al.* 2008; Reyer *et al.* 2012; Richardson and van Wilgen, 2004). However, seasonal precipitation changes influence plant phenology, including leafing out and early or late wood growth and development (Mission *et al.* 2011; Volder *et al.* 2010). Plants show a limited response to small changes in precipitation (Gerten *et al.* 2008; Miranda *et al.* 2009). The current developed framework on the effects of altered timing of rainfall events suggests that elevated rainfall would lead to enhanced runoff and deep drainage, resulting in shallow soil becoming drier and reduced plant growth (Knapp *et al.* 2008). But according to Baez *et al.* (2012) and Xu *et al.* (2012) an artificially manipulative elevated rainfall can either have a positive or negative impact on plant growth and development.

Invasive alien species response to a given change in rainfall differ, since varied reasons to expect that an increase in rainfall may intensify plant invasion exists (Dukes and Mooney, 1999). The resource hypothesis theory suggests that an increase in rainfall variability could improve the availability of water and thus facilitate plant invasion (Davis, 2000). However, invasive alien species benefit from improved water availability provided they have high water requirements. Common traits of invasive alien species that lead to high water requirements include rapid growth rates and short life spans (Saxton *et al.* 2002). The forecast that increased rainfall events will escalate plant invasion is in accordance with observations of high invasive alien plant species richness and abundance levels in regions with high moisture content (Hood and Naiman, 2000; Larson *et al.* 2001; Reever Morghan and Rice, 2006; Stohlgren *et al.* 1998). Supplementation of water with excess soil nutrients to the soil enhances the invasive alien plants to actively compete with native plants thus intensifying invasion process (Kolb *et al.* 2002; Rai, 2013).

#### 2.7. Invasive plants response to increased soil nutrients

Several studies about invasive plants have identified soil nutrient availability in abundance as a key factor in explaining their invasion (Drenovsky *et al.* 2012; Ehrenfeld, 2003; Liao *et al.* 2008). Various mechanisms involved in the acquisition and utilization efficiency of soil nutrients play a major role on invasive alien plants success (Daehler, 2003; González *et al.* 2010). Plant trait such as high phenotypic plasticity in procuring available soil nutrients frequently contributes to plant invasion success (Daehler, 2003; Sala *et al.* 2007). The plant invasion success of the relationship between invasive alien plants and the utilization of soil nutrients content differs with the soil nutrient availability. However, the increase in soil nutrient availability favors alien plant invasion when ambient soils have insufficient soil nutrients (Davis, 2000). Plant nutrient availability is stimulated by

metabolic activities of micro-organisms because of increasing soil temperature (Onwuka, 2016). Furthermore, alien plants invasion in soil nutrient-rich environments frequently favors those invasive alien plant with high photosynthetic, growth and development rates (Baruch and Goldstein, 1999; Feng et al. 2011; Feng et al. 2008; González et al. 2010; Leishman et al. 2007; Mozdzer and Zieman, 2010; Schumacher et al. 2009). Besides, invasive alien plants can increase their symbiotic interactions with fungi by directly enhancing their capacity for soil nutrient acquisition and by hindering native plants germination and growth (James et al. 2010; Zabinsky et al. 2002). A higher capacity of nitrogen acquisition is beneficial for invasive alien plants since they succeed through the facilitation of the synthesis of nitrogen-rich allelopathic compounds that restrict the growth and development of native plants (Hewins and Hyatt, 2010). Nitrogen fixing plants takes an advantage in nitrogen-poor soils dominated by non-fixing plants (Hughes and Denslow, 2005; Londsdale et al. 1989; Morris et al. 2011; Yelenik et al. 2004). A high capacity to supply and allocate nitrogen nutrients to photosynthesis process benefits invasive alien plants success in soil nutrient-rich and poor areas as well (Feng et al. 2008, 2009; Matzek, 2011). Therefore, the rate of invasion by invasive alien plants will be enhanced because of soil nutrient supplementation under the global climate change scenarios. Acacia species such as Acacia sieberiana have higher accumulated nitrogen concentration because of their atmospheric fixing ability (Chidumayo, 2008).

# 2.8. Influence of Acacia mearnsü invasion on chemical soil properties

Plant invasion is associated with both direct and indirect impacts on soil chemistry (Wekhanya, 2016). The impacts are seen on soil chemical essential constituents including soil PH, nitrogen, and phosphorus (Simba et al. 2013). Acacia species has the potential to influence the soil chemical properties which then cause an impact on the vegetation communities (Van Der Waal, 2009). Previous studies by Musil et al. (1990) and Yelenik et al. (2004) showed that soils that are invaded by highly competitive Acacia species have high nutrients, potassium, manganese, and nitrogen cycling rates resulting from high biomass and increased Acacia leaf litter decay. Soil chemistry alterations play a fundamental role on plant invasion (Sardans et al. 2017). Studies done on the effects of invasive Acacia sieberiana on soil properties and plant diversity highlighted that soil chemical properties (soil pH, Ca, N, and CEC) are found to be significantly higher under invaded soils than uninvaded soils (Mugunga et al. 2013). Invasive plants such as Eucalyptus, a successful soil nutrient competitor woody invasive plant is associated with more severe effects on soil properties as it depletes soil resources (Gupta, 1993; Guo et al. 2002; Harrison et al. 2000; Kidanu et al. 2005). In some circumstances, some invasive plants are seen to be the best improver of soil pH level but simultaneously inducing devastating impacts on plant diversity (Mugunga et al. 2013). Soils underneath the growth of a variety plant canopies are often associated with higher levels of accumulated vital soil nutrients (soil P and N) (Belksy et al. 1993; Dowling et al. 1986; Everret et al.

1986; Tiedemann *et al.* 1993). Plant litter from *Acacia* species has a huge contribution to soil fertility through its nitrogen fixation ability (Dunham, 1989).

## 2.9. Influence of future predicted climate change scenarios on soil chemical properties

Climate change has got varied influence e.g. stronger or weaker influence on soils that can be temporal or permanent. Extreme rainfall events following changes in climate results in loss and reduced soil nutrient concentration levels for example, water soluble nutrients (magnesium and calcium) (Tang *et al.* 2008; Zougmore *et al.* 2009). In addition, frequent extreme rainfall events make the soil to become waterlogged which makes it unfavourable for plant productivity (Karmakar *et al.* 2016). It is further highlighted that severe rainfall events with high intensity and amount leads to enhanced soil erosion rates for example, increasing annual rainfall with 1% increases soil erosion rate by at least 1,7% (Nearing *et al.* 2004). Intense soil surface warming resulting from extreme temperature event induces faster soil nutrient acquisition to take place by approximately 100 to 300% and plants growing on the particular soil tends to acquire more water-soluble nutrients (Ca and Mg) as temperatures readily increase (Ching *et al.* 1979; Mackay *et al.* 1984). However, the effects of extreme temperature events on soil surface depends on soil moisture availability (Karmakar *et al.* 2016).

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# Chapter 3: Quantifying germination and growth trends of invasive *Acacia mearnsii* to predicted future elevated temperature, rainfall, and soil nutrients.

#### Abstract

Climate change scenarios and plant invasion are two fundamental research priorities in ecology in the modern world. This study examined future shifts in germination, growth, and development of invasive Acacia mearnsii under predicted future global climate change scenarios. The study exposed soils, planted with the above-mentioned invasive alien plant to different artificially manipulated (i) elevated soil surface temperature (+2°C), (ii) increased (+3 mm) and decreased (+0.75 mm) rainfall, (iii) increased soil nutrient content ( $\pm 10 \text{ g/m}^2$ ), and (iv) their combined interaction in a pot and microcosm experimental system. Climate change scenarios were artificially manipulated in experimental microcosm chambers to analyze their future effects on the problematic invasive A. mearnsii. Percentage seed germination rates of invasive A. mearnsii were significantly (P < 0,001) higher in all the treatments except for low rainfall. The interaction between treatments and months showed significant (P < 0,001) differences in plant shoot heights. However, the interaction between treatments and months showed no significant differences (P > 0, 05) in the number of branches. Individual treatments accumulated significantly (P < 0,001) higher root length than combined interaction treatments. Similarly, study results showed significantly (P < 0,001) higher total dry biomass in individual treatments than in combined interaction treatments. The study concludes that possible increase of future predicted climate change scenarios significantly enhances the invasiveness of A. mearnsii germination, growth, and development.

**Keywords:** Climate change scenarios · Plant invasion · Seed germination · Acacia mearnsii · Elevated soil temperature · Microcosm

## **3.1. Introduction**

In an increasingly globalized world, the number of invasive alien species invading native plant communities continues to rise (Van Kleunen *et al.* 2015). South Africa has one of the largest emerging problems of invasive alien plants, with millions of hectares of land having been invaded (Richardson and van Wilgen, 2004; van Wilgen *et al.* 2020; Vilà *et al.* 2011). Blackburn *et al.* (2011) define invasive alien species as species that have been translocated beyond the limits of their natural range and that has established a population in a new area, become invasive where it was not known to occur previously and can cause socio-economic and environmental harm. Furthermore, Richardson *et al.* (2000) define it as a species that can present the stable populations for at least over 10 years in invasive territory and have the potential to spread across the extended regions. An introduced species

become invasive when it becomes extremely abundant and change vegetation structure (Blackburn, 2011; Iponga *et al.* 2008) and out-compete native plant species for available vital resources such as light, soil nutrients, light, physical space, and available water (Lockwood *et al.* 2007; van Klinken *et al.* 2006). Once spread in a new ecosystem, invasive alien species threaten biodiversity mostly through its possible traits that are linked to invasiveness including highly competitive abilities, high phenotypic plasticity, high growth rates, broad climatic tolerance, and genomic pool size (Castro-Di'ez *et al.* 2011; Davidson *et al.* 2011; Kubešová *et al.* 2010; Lamarque *et al.* 2011; Sakai *et al.* 2001; Vila and Weiner, 2004; Walther *et al.* 2009).

In South Africa, much of the historic concern about invasive alien plants relates to the devastating consequences for biodiversity conservation by displacing native plants biological properties resulting in species richness reduction and extinction (Butchart et al. 2010; Mamba et al. 2019; Ossom et al. 2007; Vilà et al. 2011). Invasive Acacia species are known to have adverse negative impacts on the invaded plant communities and ecosystems by creating an imbalance in the ecosystem (Colautti and MacIsaac, 2004; Vila et al. 2009). For example, Australian Acacias (commonly known as wattles) are associated with negative impacts on soil forming factors, nutrient cycling, and depleting water resources (Bromilow, 2010; Le Maitre et al. 2011). Other invasive species, e.g. Opuntia species have the potential to form dense impenetrable monospecific stands barrier restricting access to wild animals compared to native plants (Mamba et al. 2019; Van Klinken et al. 2006). They also induce interference on agricultural, rangelands, and commercial forestry industries (Dlamini, 2010; Vil et al. 2010). For example, they invade crop fields resulting in reduced crop harvest and more capital is required to manage the invaders (Bromilow, 2010; Rijal and Cochard, 2016). Some invasive alien species such as Acacias and Chromolaena odorata, depending on the invaded area, are associated with health issues. For example, they make human societies vulnerable to health hazards such as induced veld fire intensity since they are highly flammable (Rodgers et al. 2017; Shackleton et al. 2007). However, not all invasive alien species are considered detrimental because some have no adverse effect (Didham et al. 2005; van Wilgen and Richardson, 2014). For example, introduction of some invasive alien plants is beneficial to the native species by providing them with food resources and shelter (Schlaepfer et al. 2011). People and wild animals benefit from edible berries produced by a highly invasive Himalayan blackberry. In addition, it is widely used for landscaping (Mamba et al. 2019). Similarly, *Eucalyptus* species are a huge benefit to the forest and bee industry in South Africa (Hirsch et al. 2020). In some cases, they provide food sources that act as natural capital through their sales (Shackleton et al. 2011, 2019).

The relationship between plant invasion and climate change scenarios is complex (Grigulis *et al.* 2005; Myers *et al.* 2004). Climate change scenarios are likely to enhance the dimensions of invasive

alien species to invade and occupy new regions, while simultaneously increasing their adaptability in natural communities by disturbing the dynamic equilibrium maintaining them (Walther *et al.* 2007). In addition, invasive alien plants influence the magnitude, rate, and impact of climate change scenarios by altering ecosystem composition, structure, and functioning (Pyšek *et al.* 2010). Previous reports have reported that global warming is expected to result in poleward and altitudinal shifts in plant ranges (IPCC, 2007; Parmesan and Yohe, 2003; Root *et al.* 2003). The above-mentioned report by IPCC also forecasts that many ecosystems will become vulnerable to plant invasions as climatic barriers are disrupted. Furthermore, the IPCC predicts that an increase of greater than 1.5 - 2.5°C in the global average temperature will cause dramatic changes in species distribution and ecosystem function, resulting in overwhelmingly negative consequences for ecosystem sustainability (IPCC, 2007). Furthermore, climate change scenarios have the potential to determine the type of plants that can grow and develop at a certain region based on temperature and precipitation quantity (Banwart, 2011; Bauer *et al.* 1996).

Climate change scenarios exert a dominant control on the natural distribution of plant species and biodiversity (Schroter *et al.* 2005; Pearson *et al.* 2003; Vitousek, 1994), as well as the risk of plant species extinction (Sala *et al.* 2000; Thomas *et al.* 2004). Parry *et al.* (2007) revealed that observational evidence across the continents shows that many natural systems are being disrupted by regional climate change scenarios, mostly elevated temperature. However, some scholars do not agree on the exact predictions from different models (Hultine *et al.* 2013). It is evident that by the end of the  $21^{st}$  century, average increased temperature around the world is expected to have risen by approximately  $0.3 - 4.5^{\circ}$ C (Stocker *et al.* 2013). It is also evident on the synthesis report of the Fifth Assessment Report of the IPCC that since 1850 temperature is progressively increasing every decade due to globalization (IPCC, 2014).

Impacts of elevated temperature on plants traits mainly modify phenology, growth, development, productivity, and major physiological processes that sustain the plant (Jamieson *et al.* 2012). For example, elevated temperature is a key factor that advance vital plant phenological processes that influences plant growth (Rennenberg *et al.* 2006; Wang *et al.* 2012). Previous literature indicates that plant growth and development strongly improve with increasing temperature (Norby and Luo, 2004). Following that it has been further reported that invasive alien plants perform better under extremely high temperature conditions at an overall of warming of 40/35°C. This shows that extreme temperature events increase the risk of plant invasion since invasive alien plants seedlings were able to establish under that condition compared minimum temperatures (Chen *et al.* 2014). Moreover, all plants require adequate temperature for growth and development (Prentice *et al.* 1992). Previous meta-analysis of plant responses to experimental manipulated warming by Rustad *et al.* (2001) further

explains that temperature enhances plant productivity. Moreover, consistent literature indicates that plant responses vary with individual species and climate change scenarios and how they interact (Kirschbaum, 2000).

Extreme warming during dry seasons induces the intensity and frequency of water stress periods that may lead to plant mortality at early stage (McDowell et al. 2011). Rainfall is regarded as a vital environmental factor that drives the survival of woody plants; it is however driven by climate change scenario alterations (Scholes et al. 1997). In Southern Africa Savanna biomes, climatological data predictions proposed a decrease with rates ranging between 5 - 15% in the average annual rainfall by 2050 (IPCC, 2001). Moreover, a previous study also reported a consistent increase in the variability and frequency of elevated rainfall events typical in Southern Africa regions (Tyson, 1987). The predictions by the IPCC (2013) have revealed that fluctuations in rainfall events are expected to be less constant. Rainfall regimes are crucial determinants for all plant traits such as plant growth, reproduction, and mortality (Hennon et al. 2012). Several studies regarding invasive alien plants have identified soil nutrient availability as a key factor in explaining their invasion success (Drenovsky et al. 2012; Ehrenfeld, 2003; Liao et al. 2008). Various mechanisms involved in the procuring and efficiency use of soil nutrients plays a major role in invasive alien plants success (Daehler, 2003; González et al. 2010). For example, Funk (2013) study further suggested that invasive alien plants are most likely to survive in conditions where there is sufficient nutrient acquisition, but plant nutrient requirement differs with plant species. In this context of climate change, this indicates that climate change scenarios will continue to enhance the spread and distribution of woody invasive alien plants (Parmesan, 2006). However, previous literature indicates that in Southern Africa biomes, climate change scenarios are the crucial environmental parameters driving woody plants distribution (Tews et al. 2004). For example, invasive Acacias have been described as transformers (Souza-Alonso et al. 2017), which (Marchante et al. 2011; Richardson et al. 2000) has described transformers as invasive alien plants that "substantially alter the character, condition, nature of ecosystems, becoming active agents in region-forming processes".

Acacia mearnsii is a fast-growing leguminous, nitrogen-fixing tree that belongs to the Fabaceae family (Moyo and Fantubi, 2010). The plant is amongst the worst problematic invasive alien plants in South Africa (Dye and Jarmain, 2004). It is commonly known as an Australian Black Wattle, many see it as a highly destructive invasive alien plant (Beck and Dunlop, 2002). *A. mearnsii* is prevalent on the South-Eastern Australia (its native range; Dunlop, 2002), where it has been grown mainly for timber production and tannin extraction from its barks (Chan *et al.* 2015). The species was introduced to South Africa in the year 1864 (Nyoka, 2003), mainly for fuelwood, shade, windbreaks, and commercial source of tannin content of its barks (Campbell, 2000; Le Maitre *et al.* 2011; Stinson

et al. 2006). Furthermore, it is grown as a commercial forestry plant species with at least approximately 7.6% of the total area owned by the commercial forestry plantations companies in South Africa (Forestry South Africa, 2009). To date, the species invaded more than 110 000 ha of land in South Africa (Feely, 2012), predominantly in the regions of KwaZulu-Natal and Mpumalanga province (Chan et al. 2015), and in addition to that it is viewed as a major invader in South Africa. However, it is rated as number eleven in the invaders' list in the fynbos biome, fifth in the KwaZulu Natal and sixth in Gauteng Province (Nyoka, 2003). Richardson et al. (2000) and Le Maitre et al. (2002) note that in the Western Cape province the plant has outcompeted native plants along riparian zones as the plant has the potential to germinate, grow and develop dense thickets that are impenetrable and evergreen. Acacia mearnsii is known to flourish better along most riparian zones including disturbed river systems in South Africa (Maoela, 2015; Moyo and Fantubi, 2010; Versfeld et al. 1998). In addition, the plant flourishes in both natural and agricultural lands (Kutiel et al. 2004; Henderson, 2007; Marchante et al. 2011). Moreover, the plant is also able to grow under drought conditions with scarce water and nutrient availability due to its extensive root system mechanism (Crous, 2010; Rodriguez-Echevarria, 2011; Sprent, 2009), although it mostly prefers moist regions with deep fertile soils (Crous, 2010).

Acacia mearnsii produces large number of seeds that remain dormant and get activated by veld fires leading to maximum germination rate percentages, producing matured plants that successfully grow and develop enormous shade that engulf native plants (Moyo and Fantubi, 2010). Pretorius *et al.* (2008) explain that it is influenced by its small seeds which enables them to remain in the soil for approximately 60 years. It is a tremendous threat to the natural vegetation especially native diversity, since it forms thickets, and the variety of native plants are replaced by its monospecific stands that are dense and evergreen (Nyoka, 2003). Furthermore, the plant has highly competitive rates for resources mainly for growth and development including water, soil nutrients and symbiotic nitrogen fixing (Crous, 2010; Le Maitre *et al.* 2011). According to Witkowski (1991) and Moyo and Fantubi (2010), areas invaded by the plant are covered with great mass of leaf litter which hinders native seedlings to acclimatize, grow, and develop under this overwhelming condition.

In South Africa, the species is listed under category 2 invader (plants that are grown under controlled conditions in permitted zones and cannot be traded) (DFFE, 2016). The thick evergreen impenetrable stands of the species can grow to a height ranging from of 1 to 20 m compared to native riparian plant communities, making it the tallest *Acacia* species comparing with other *Acacia* species e.g. *A. Saligna, A. longifolia* and *A. cyclops* (DWEA, 1997; Rascher *et al.* 2012), and it flowers in the winter season (Campbell, 2000). *Acacia mearnsii* is a light-demanding species, which is sensitive to fire during young developing stage (Bromilow, 1995). The commercial plantation industries promote the

use of *A. mearnsii* as a potential soil improver (Rejmanek, 1995). For example, invasive *A. mearnsii* is used as an effective soil stabilizer to reduce the rate of soil erosion. It has some known medical applications such as its use as an astringent or styptic (Rouget *et al.* 2002). Adaptability and survival of invasive *A. mearnsii* to both favorable and harsh environmental tolerance with rapid seed germination and growth rates will more likely favor its future invasion trends, spread and distribution under future predicted climate change scenarios (Maslin and McDonald, 2004).

In this regard, experimental studies on individual and interactive effects of future climate change need to be conducted on problematic invasive plants such as *A. mearnsii*. It is important to examine and observe how plant species respond to experimentally manipulated extreme warming, rainfall, and soil nutrients since it is vital for a more up to date understanding of the results of effects of climate change scenarios (Cowles *et al.* 2018). Therefore, this study is motivated by the need to gather information on invasive *A. mearnsii* response to future climatic changes. This might aid in predicting its future invasion trajectory. *A. mearnsii* is selected because it is a well-known problematic invasive alien plant causing devastating ecological and economic effects in South Africa (Richardson *et al.* 2007). Results of this experiment could provide useful predictions of potential climate change scenarios impacts that could guide invasive *A. mearnsii* control and management in South Africa. Also, the study might help in understanding the underlying ecological properties of alien invaded communities in response to climate change scenarios. This understanding may allow researchers to predict changes in community structure.

The aim of this study was to examine future shifts in the germination and growth of invasive A. *mearnsii* under predicted future global climate change scenarios. The specific objectives are to examine (i) how elevated temperature ( $\pm 2^{\circ}$ C increase) affect germination and growth of invasive A. *mearnsii*, (ii) how high (above local average) and low (below local average) precipitation affect germination and growth of invasive A. *mearnsii*, (iii) how elevated temperature ( $\pm 2^{\circ}$ C increase) affect germination and growth of invasive A. *mearnsii*, (iii) how elevated soil nutrient content (increase in soil N) affect germination and growth of invasive A. *mearnsii*, and (iv) how a combination of the above treatments affect germination and growth of invasive A. *mearnsii*.

# 3.2. Study hypothesis

The study hypothesizes that germination, growth, and development of invasive *A. mearnsii*, will be enhanced by elevated temperature, rainfall, and soil nutrients. For example, increased rainfall and soil fertility will increase growth of *A. mearnsii*. The hypothesis is based on the suggestion that most invasive alien species have the potential to adapt to different climatic conditions. Besides, invasive alien plants can utilize excess resources (resource opportunities hypothesis) and occupy underutilized

disturbed niche (niche opportunities hypothesis) in the new ecosystem. These above-mentioned two theories have the potential to facilitate further invasion under future global climate change scenarios.

#### 3.3. Methods

#### **3.3.1. Experimental design**

The study was a greenhouse-based experiment conducted at Rhodes University, in Makhanda (formerly Grahamstown), South Africa. The passively ventilated greenhouse at Rhodes University, allowed air temperatures to be closely approximated to outside temperature. In this greenhouse-based experiment, temperature, rainfall, and soil nutrients were manipulated to simulate future global climate change scenarios. The experimental design comprised of 180 plant pots under different climate change scenarios and 12 microcosm chambers (each measuring 1 m long x 45 width x 15 cm high). Soils were collected at the Bathurst area, just outside Makhanda, on uninvaded sites (areas that are dominated by natural vegetation). Soils were collected using a soil core measuring 15 cm diameter at 10 cm depth. Soils were collected 5 m apart with the first collection point starting 5 m into the uninvaded area.

Collected soils were transferred into germination pots of the same above-mentioned dimensions as the soil cores. After collection, soils were transferred to a greenhouse for preparation and soil sterilization process. Soil sterilization was conducted by sieving collected field soils through a 2 mm mesh to remove all the debris, rocks, plant litter, and the seeds. The soils were then oven-dried at 120°C for two days and left to dry. Soil sterilization aimed to get rid of all soil biota to make sure that the soils are germ-free. After soil sterilization, each plant pot was filled with 500 g of sterilized soils. The pots were placed in the chambers, each with 15 pots. Each chamber, made of plastic containers, was 1 m long x 45 wide at a depth of 15 cm.

Forty-five seeds of the invasive plant *A. mearnsii* were sown in each treatment thus three seeds per plant pot initially, and the density was reduced to one seedling per pot after germination. The treatments were: first, high-temperature treatment which was achieved by suspending one infra-red lamps at 1.2 m from the chamber with the pots. Each high temperature experimental chamber received a downward radiant flux of 175 Watts per square meter supplied by suspending Philips incandescent 230V PAR38 infrared lamps, thus the infra-red lamps elevated soil temperature of +2°C above ambient that is consistent with future South African climate change scenarios (DFFE, 2017). Furthermore, changes in temperature were detected by making use of the Ibuttons, product thermocron (-40°C to 85°C) Acc 1°C, that is enclosed inside the silicone waterproof enclosure, two Ibuttons were placed under the soil with energized infra lamps, two Ibuttons placed under the soil with no infra-red lamps and one Ibutton on the soil surface. Second, high rainfall treatment was

achieved by watering 15 pots in a chamber with water two times a week with above (x2) average daily precipitation of 3 mm. This was done to simulate a future increase in rainfall. Third, low rainfall treatment was achieved by watering 15 pots in a chamber with water two times a week with half of the average daily precipitation of 1.5 mm. This was meant to simulate a future decrease in rainfall. Calculations for both high and low rainfall estimates were done using the average daily rainfall for 2017 and 2018 for the study area, using the standard rainfall amount for daily amounts. Fourth, increased soil nutrients treatment was achieved by adding N-P-K fertilizers which are rich in N to the soils in fifteen of the plant pots, elevated nitrogen fertilizer rates were calculated at 10g/m<sup>2</sup> based on suggestions by Nadeem *et al.* (2010). Fifth, a combination of increased temperature, high rainfall, and increased soil nutrient content treatment was administered on 15 plant pots in a chamber. Sixth, a combination of increased temperature, low rainfall, and increased soil nutrient content treatment was administered on 15 plant pots in a chamber. The control received normal watering amounting of 1.5 mm. Throughout the experiment watering of the seedlings was done after every second day, to avoid waterlogging conditions, maintaining soil moisture, and allowing the seedlings to grow and develop.

## 3.3.2. Data collection

In each plant pot, germination percentages were recorded after one month of germination. The germination rate was calculated as the total number of seedlings that germinated per pot in comparison to the total number of seeds planted expressed as a percentage. Seedling growth rates (plant shoot height) were measured each month from January to May 2020 in centimetres (cm) using a ruler. On a monthly basis, the numbers of branches emerging per seedling were counted. At the end of the experiment, the seedlings were harvested, and their root length and total dry biomass were measured. Soils were carefully washed from the roots and root length was measured in centimetres (cm) for each seedling. To measure dry biomass, the harvested seedlings were then dried at 105°C for two days and weighed with a scale to determine the total dry biomass in grams (g).

#### 3.3.3. Data analysis

All statistical analyses were performed using TIBCO Statistica version 13.5.0.17 (Software Inc, 2019). Proof of normality and homogeneity of variance was tested using Kolmogorov-Smirnov and Lilliefors test, respectively. Data were normally distributed. The effect of climate change scenarios (temperature, rainfall, soil nutrients, and combined interactions with low and high rainfall) on seed germination rate, number of branches, root length, and total dry biomass of *A. mearnsii* seedlings were assessed by one-way ANOVA at P < 0.05 since data were collected once. Data were assessed for all effects by treatments namely, high temperature, low rainfall, high rainfall, high nitrogen, combination treatment (low rainfall), combination treatment (high rainfall), and control. Tukey

Unequal N HSD post hoc tests for homogeneous groups were performed to determine the differences between the treatments. Factorial Anova was used to analyse the effects the different treatments on seedling growth (plant shoot heights) and the number of branches of *A. mearnsii* seedlings. Factorial Anova was used because data were collected monthly from January to May. Tukey Unequal N HSD post hoc tests for homogeneous groups were performed to determine the differences between treatments × months interaction.

#### 3.4. Results

## **3.4.1. Plant germination**

There were significant (P < 0.05) differences between both individual and combined interaction treatments compared with the control with respect to percentage seed germination rate of *A. mearnsii*. The results showed that the seed germination rate was significantly higher in high rainfall treatment, whereas low rainfall treatment accumulated a lower seed germination rate compared to the control (Figure 1). Contrary to that, both the high-temperature treatment and elevated nitrogen treatment showed a significantly (P < 0.05) higher seed germination rate compared to the control. Both combined low and high rainfall treatments showed a significantly significant differences (Figure 1).



Figure 1. Results show the percentage seed germination rate of invasive *A. mearnsii* for both individual and combined interaction treatments relative to control. Error bars represent the mean  $\pm$  SE for each treatment, and one-way ANOVA results are shown. Bars with different superscripts are significantly different at *P* < 0.05.

#### 3.4.2. Plant growth

There were significant (P < 0.001) differences between all the treatments, months, and interactions between treatment and months for plant shoot height (Tables 1 and 2). High-temperature treatment significantly improved plant shoot height from 3,87 cm  $\pm$  0,98 (January) to 14,90 cm  $\pm$  1,66 (May). Percentage shoot height over the experimental months was significantly different with an overall change of about 22%. (Table 1 and 2). Similarly, low rainfall treatment significantly improved plant shoot height from 1,90 cm  $\pm$  0,41 in January to 11,43 cm  $\pm$  1,95 in May. The above-mentioned percentage changes over the experimental months were significantly different with an overall change of approximately 32% (Table 1 and 2). Also, high rainfall treatment significantly improved plant shoot height from 4.43 cm  $\pm$  0.60 (January) to 13.43 cm  $\pm$  1.38 (May), percentage changes over the experimental months accumulated an overall change of 20,30% (Tables 1 and 2). In contrast, high nitrogen treatment significantly improved plant shoot height from 1,27 cm  $\pm$  0,22 (January) to 5,07 cm  $\pm$  1,26 (March) (P < 0.05); and percentage changes were significantly different with an overall change of 38,89%. This is a magnitude of change of four-fold between January and March, however, there were no changes in plant shoot heights between March and May (Tables 1 and 2). Combined low rainfall treatment significantly improved plant shoot height from 1,41 cm  $\pm$  0,26 in January to 5,73 cm  $\pm$  1,12 March. Between January and March, the percentage changes in combined low rainfall treatment were significantly different with an overall change of 41,54%, but a consistent trend was observed between March and May with no change (Table 1 and 2). A similar trend was observed in combined high rainfall treatment that significantly improved plant shoot height from 1,43 cm  $\pm$  0,21 to 4.57 cm  $\pm$  1.05. Percentage changes over the early experimental months were significantly different from January to March with an overall change of 31,94 % and a consistent trend was observed between March and May with no change (Table 1 and 2). In the control treatment (normal rainfall, temperature, and nitrogen) plant shoot height significantly improved from 2,71 cm  $\pm$  0,21 in January to 15,11 cm  $\pm$  0,68 in May, percentage changes over the experimental months had an overall change of about 27% (*P* < 0.05, Tables 1 and 2).

There were significant (P < 0,001) differences between all the treatments and months for the number of branches (Table 1 and 2). However, the interaction between treatments and months showed no significant differences in the number of branches (Table 1 and 2). Seedlings in the high-temperature treatment accumulated a greater mean number of branches in the early months of the experiment from  $4,87 \pm 1,03$  in January to  $5,93 \pm 0,56$  in May. A similar trend was observed in low rainfall treatment with an increasing number of branches over the first four months of the experiment and a drop over the last month (Table 1). In the early months of the experiment, high rainfall treatment seedlings had an increasing number of branches towards the mid months (January to March) from  $4,67 \pm 0,40$  to  $6,40 \pm 0,58$ , but with a decreasing trend towards the late months (April to May) of the experiment from  $4,87 \pm 0,53$  to  $4,73 \pm 0,49$ . In contrast, the high nitrogen treatment accumulated a greater number of branches in the early months, rising from  $2,33 \pm 0,41$  in January to  $5,47 \pm 0,65$  in March and no changes in number of branches were recorded between March and May. Combined low rainfall treatment seedlings had a greater number of branches in the early months of the experiment increasing from  $1,80 \pm 0,34$  in January to  $4,53 \pm 0,46$  in March. No changes were observed between March and May. A similar trend followed on combined high rainfall treatment seedlings that accumulated a greater number of branches at the early months (January to March) of the experiment  $1,80 \pm 0,28$  to  $3,87 \pm 0,54$  and a consistent number of branches from the mid towards late months (March to May) of the experiment  $4,93 \pm 1,03$ . However, control treatment seedlings accumulated the greater number of branches over the first four experimental months (January to April) from  $4,43 \pm 0,39$  to  $6,21 \pm 0,38$ and a drop over the last month (May) of the experiment  $5,98 \pm 0,40$  (Table 1 and 2).

**Table 1.** Comparisons of plant shoot heights and number of branches of different climate change scenarios treatments in different months from January to May 2020. Data are means  $\pm$  SE and two-way ANOVA results are shown in Table 2. Different superscripts indicate statistically significantly different at *P* < 0,05.

	Mean plant shoot height (cm)						Mean number of branches							
Month	HT	LR	HR	HN	CLR	CHR	С	НТ	LR	HR	HN	CLR	CHR	С
Jan	3,87	1,90	4,43	1,27	1,41	1,43	2,71	4,87	3,13	4,67	2,33	1,80	1,80	4,43
	±	±	±	±	±	±	±	±	±	±	±	±	±	±
	0,98ª	0,41 <sup>b</sup>	0,60ª	0,22 <sup>b</sup>	0,26 <sup>b</sup>	0,21 <sup>b</sup>	0,21 ª	1,03ª	0,65ª	0,40 <sup>a</sup>	0,41 <sup>b</sup>	0,34 <sup>b</sup>	0,28 <sup>b</sup>	0,39 <sup>b</sup>
							b							
Feb	6,45	2,91	5,57	3,43	3,26	3,83	5,76	5,47	4,93	6,40	6,40	3,80	3,87	6,34
	±	±	±	±	±	±	±	±	±	±	±	±	±	±
	0,59ª	0,67 <sup>d</sup>	0,65 <sup>abc</sup>	0,49 <sup>bcd</sup>	0,61 <sup>cd</sup>	0,56 <sup>bcd</sup>	0,32 <sup>ab</sup>	0,35ª	0,84 <sup>b</sup>	0,58ª	0,58ª	0,55 <sup>b</sup>	0,54 <sup>b</sup>	0,43ª
March	11,40	5,23	8,73	5,07	5,73	4,57	9,53	6,47	6,13	4,87	5,47	4,53	4,93	6,07
	±	±	±	±	±	±	±	±	±	±	±	±	±	±
	1,22ª	1,14°	1,08 <sup>bc</sup>	1,26°	1,12 <sup>bc</sup>	1,05°	0,48 ª	0,35ª	0,95ª	0,53 <sup>b</sup>	0,65 <sup>ab</sup>	0,46°	1,03 <sup>b</sup>	0,42ª
							b							
April	13,53	8,53	12,17	5,07	5,73	4,57	12,67	6,40	6,53	5,20	5,47	4,53	4,93	6,21
	±	±	±	±	±	±	±	±	±	±	±	±	±	±
	1,34ª	1,71 <sup>ab</sup>	1,13ª	1,26 <sup>b</sup>	1,12 <sup>b</sup>	1,05 <sup>b</sup>	0,76 <sup>a</sup>	0,51ª	1,14 <sup>a</sup>	0,51 <sup>b</sup>	0,65 <sup>b</sup>	0,46 <sup>b</sup>	1,03 <sup>b</sup>	0,38ª
May	14,90	11,43	13,43	5,07	5,73	4,57	15,11	5,93	6,27	4,73	5,47	4,53	4,93	5,98
	±	±	±	±	±	±	±	±	±	±	±	±	±	±
	1,66ª	1,95 <sup>b</sup>	1,38ª	1,26°	1,12°	1,05°	0,68ª	0,56ª	0,93ª	0,49 <sup>b</sup>	0,65ª	0,46 <sup>b</sup>	1,03 <sup>b</sup>	0,40ª

Letters are HT = High temperature, LR = Low rainfall, HN = High nitrogen, HR = High rainfall, CHR = Combined high rainfall, CLR = Combined low rainfall, and C = Control.

**Table 2.** Two-way ANOVA results showing the effects of different climate change scenarios treatments on plant shoot heights and the number of branches through treatments, months, and the interaction between treatments and months.

	Two-way ANOVA								
	Treatment	s	Months		<b>Treatments x Months</b>				
	F-value	P-value	F-value	P-value	F-value	P-value			
Mean plant shoot height (cm)	50.625	0.001	76.079	0.001	4.708	0.001			
Mean number of branches	14.515	0.001	22.534	0.001	1.264	0.178			

# 3.4.3. Root length and total dry biomass

Relative to the control, both individual and combined interaction treatments showed statistically significant (P < 0.05) differences in *A. mearnsii* seedlings root length (Figure 3). After the termination

of the experiment, high-temperature treatment seedlings accumulated a significantly lower root length with a difference of 1 cm compared to the control. A similar trend was evident in both low and high rainfall treatments seedlings that accumulated significantly lower root length compared to the control, but low rainfall seedlings had a difference of 5,4 cm while high rainfall seedlings had a difference of 1,2 cm compared to the control. However, high nitrogen treatment seedlings also accumulated a significantly lower mean root length with a difference of 10,4 cm compared to the control. Contrary to that, both combined low and high rainfall treatments seedlings accumulated a significantly lower root length compared to the control. However, combined low treatment had a lower difference of 8,4 cm whereas combined high treatment seedlings had a higher difference of 11,4 cm compared with the control treatment seedlings (Figure 2).



Figure 2. Response of *A. mearnsii* root length to climate change scenarios. Error bars represent the mean  $\pm$  SE per each treatment and one-way ANOVA results are shown. Bars with different superscripts are significantly different at *P* < 0.05.

Both individual and combined interaction treatments showed statistically significant (P < 0,05) differences in *A. mearnsii* seedlings total dry biomass relative to the control (Figure 3). At the termination of the experiment, high-temperature treatment seedlings accumulated significantly higher total dry biomass with a difference of 0,1 g than the control treatment seedlings. However, total dry biomass was significantly lower in both low and high rainfall treatments seedlings (both 0,4 g) than in the control treatment seedlings. Similar patterns were observed for high nitrogen treatment, with both

combined low and combined high rainfall treatments seedlings showing significantly lower total dry biomass than the control (Figure 3).



**Figure 3.** The response of *Acacia mearnsii* total dry biomass to climate change scenarios. Error bars represent the mean  $\pm$  SE, *n*=15 per each treatment and one-way ANOVA results are shown. Bars with different superscripts are significantly different at *P* < 0,05.

## 3.5. Discussion

## 3.5.1. Effects of global climate change scenarios on plant germination

In plant life cycle, seed germination is an important factor that drives the seedling establishment, and growth which then predicts whether the plant seedling will be able to acclimatize and survive harsh environmental conditions (Khan, 1971). Experimental manipulation of climate change scenarios (high temperature, rainfall, and nitrogen) had a great variation and some consistent trends in seed germination rate percentages of *A. mearnsii* seedlings. The experiment showed that elevating temperature, rainfall, and nitrogen individually aid *A. mearnsii* seed germination. For example, except for low rainfall treatment, results showed that high temperature ( $+2^{\circ}C$ ), high rainfall (3 mm), high nitrogen (10 g/m<sup>2</sup>) and combined treatments (low and high rainfall) resulted in enhanced seed germination rate for *A. mearnsii* seedlings. The results indicate that all the treatments tested, except low rainfall, achieved > 50% germination rate. The findings under elevated climate change scenarios are consistent with the previous findings by Erfmeier and Bruelheide (2005) who found that invasive alien plants exhibit higher seed germination rate as one of the characteristics that make plant invasion a success, this gives a good explanation for the study species *A. mearnsii*.

A higher seed germination rate of A. mearnsii under high rainfall amounts suggests that it is a faster germinator when there is frequent maintenance of soil moisture. These findings are consistent with the previously reported findings by Jurado et al. (1992). A lower seed germination rate under low rainfall treatment is perhaps explained by the fact that under limited rainfall amounts, seedling establishment mostly relies on seed mass and size (Moles et al. 2004; Muller-Landau, 2010). Similar findings by Donohue (2005), Simons et al. (2000), and Hoyle et al. (2015) provide strong evidence that low rainfall is an unfavourable environmental condition for the seedling establishment which leads to seedling mortality at an early stage (Brooks, 1998). Low seed germination in the low rainfall treatment could be explained by soil surface layers drying very quickly, and this hinders the seed germination process disproportionately. Choinski et al. (1991) reported consistent findings of low rainfall amounts. For example, they reported that Acacia species showed a repeatedly reduction in seed germination rate in response to unfavourable condition of low rainfall events whereas African plant species such as Combretum apiculatum and Colosphermum mopane were found to tolerate seed germination under stressful rainfall and temperature events. Previous studies by Engelbrecht et al. (2006) and Pearson et al. (2002) similarly reported the occurrence of progressive mortality under limited water supply for invasive Apeiba aspera species. Lower germination of A. mearnsii under low rainfall demonstrates that the species is a slow germinator under low rainfall amounts and vice versa (Jurado et al. 1992). Jurado et al. (1992) founds that seed germination decreased by 39.4% for the plant species (Shorea macrophylla and Parashorea tomentella) they considered on their study under limited rainfall events.

High temperatures are more likely to facilitate the establishment and influence the risk of intensifying the distribution patterns, spread, and prevalence of invasive alien plants (Bradley *et al.* 2010; Walther *et al.* 2009). Seed germination rates are influenced by the warming under which the seeds are curated and the fluctuations in warming are more likely to accelerate the seed germination rates (Graae *et al.* 2008). Graae *et al.* (2008) reported that seed germination proportions are positively correlated with the certain temperature under which the seeds are sown. According to Thompson (1974) and Thompson *et al.* (1977) temperature fluctuations during the day are most likely to mimic the seed germination proportions. However, Milbau *et al.* (2009) showed that moderate temperatures in the summer season have a significant extent of accelerating the germination rate percentages, although the magnitudes of plant response are dependent on a variety of species. Temperature is one of the most determinant factors that can either act separately or jointly with other factors since it plays a vital role in the periodicity of seed germination (Guan *et al.* 2009). Plant germination response to temperature depends on several factors such as the quality of the seeds, type of plant species, and the environment (Shaban, 2013). Shaban (2013) further explained that high-quality seeds have the

potential to germinate under a variety of temperature ranges as compared to low-quality seeds. The study findings agree with the above-mentioned suggestions by Shaban (2013) because in some treatments considered, for example combined treatments (low and high rainfall), high temperature integrated with other environmental factors such as rainfall and soil nutrient to enhance germination.

## 3.5.2. Effects of global climate change scenarios on plant growth

Plant species growth responds differently to climate change scenarios (Brandt et al. 2004; Marchand et al. 2006). Results of this study showed that plant shoot height, number of branches, and root length responded positively to climate change scenarios over the experimental months. For example, high temperature aided A. mearnsii seedling plant shoot height, number of branches, and root length over the experimental months. This is consistent with findings of an experimental study by Jia et al. (2016) which found that global warming has the potential to facilitate plant invasion by allowing invasive plants to perform better under high temperatures. Verlinden and Nijs (2010) and Wang et al. (2011) also support the influence of elevated warming in stimulating plant invasion by accelerating the physio-ecological characteristics and competitive ability of invasive. Similarly, a study by He et al. (2012) support that interacting elevated warming jointly with other corresponding factors such as rainfall and soil nutrients may promote plant invasion by stimulating their growth and survival in harsh environmental conditions. Temperature effects depends on the availability of rainfall for example, low rainfall has a major impact that leads to water deficits than excess rainfall on plant growth (Hatfield et al. 2015). Jia et al. (2016) and Ekselinen et al. (2014) showed that a combination of temperature, elevated rainfall and enhanced nutrients exhibits a significant impact on invasive alien plants mostly through the performance traits including plant physiology, node, and leaf appearance, shoot allocation appearance, nutrient uptake, and plant photosynthetic performances.

The plant physiological traits that play a significant role includes quality of the seeds and plant species type (Shaban, 2013). A study by Liang *et al.* (2013) reported that elevated warming has a positive effect on plant photosynthetic rates. However, high nitrogen uptake by the plant has been reported to have a great support for root growth (Postma *et al.* 2014). These findings lend support to this explanation because over the experimental months *A. mearnsii* seedling growth seemed to cope better under high temperatures and rainfall. Research conducted by Kumudini *et al.* (2014) to document the effects of elevated warming on plants also support the notion that extreme temperatures are more likely to have considerable effects on plant processes such as germination, transpiration, respiration, and photosynthesis rate increase but that depends on the plant species as it can either speed up or slow down the growth. Recent findings by Onwuka (2016) concluded that soil surface temperature is vital for the maintenance of plant life by catalysing plant biological processes, soil

moisture, and nutrient availability, thus playing a fundamental role in plant growth and development. In addition, soil warming has a fundamental influence on plant growth since it influences soil moisture content, nutrient uptake levels, plant root and shoot growth (Toselli *et al.* 1999; Weigh and Karlson, 1999).

Soil moisture is considered one of the most important limiting factors for plant growth, and development of woody plants and shrubs. Over the experimental months, rainfall treatments increased plant shoot height, number of branches, and a greater proportion of root length at the end of the experiment. A comparison between different simulated rainfall regimes showed that high rainfall had greater overall plant growth than low rainfall treatment. This study findings under high rainfall are similar to those reported in a study by O'Brien et al. (2013). Furthermore, it has been highlighted that elevated rainfall is more likely to facilitate plant invasion in altered conditions with enough nutrient availability (Eskelinen et al. 2014). In addition, greater growth under high rainfall amounts is influenced by the superficial lateral root system developed by A. mearnsii, which keeps high water holding capacity (Orwa et al. 2009). Hsiao (1973) and Barley et al. (1967) reported that developing water stress condition makes the soil surface to be low in water and become compacted which then restrict seedling root growth and enlargement, expectedly this account for this study's findings under low rainfall treatment. A good explanation for slightly less overall proportion of plant shoot height, number of branches and root length under low rainfall is that during seedling establishment stage, belowground plant parts such as seedling roots utilize less water to meet growth and development requirements leading to increased soil surface drying and disproportionately limiting seedling growth (O'Brien et al. 2013). This suggests that the invasiveness of A. mearnsii decreases as rainfall amounts lower and explains why plant growth is low under drought conditions.

However, this study findings have shown that high nitrogen and combined treatments (low and high rainfall) do not consistently improve plant shoot height, the number of branches and root length since they only showed an increase over the early months (January to February) and a consistent trend over the late months (March to May) of the experiment, as a result, the overall growth proportions were lower. An optimal theory of allocation developed by McCarthy and Equist (2007) states that plants allocate and supply more available resources to the aboveground than belowground parts, which allows them to procure additional space and light consequently increasing their competitiveness and productivity. This theory is in line with results of this study since experimental treatments showed an improvement in the aboveground plant parts such as plant shoot height and number of branches in the early growth months. The optimal theory of allocation also accounts for lower root length (belowground important plant parts) for nitrogen and combined treatments (low and high rainfall). A study by Wu (2017) reported that plant nutrients may be specifically prone or directed to be allocated

more effectively for the growth of belowground plant parts such as roots, and as a result the growth of aboveground plant parts are depressed especially when the nitrogen fertilizer levels are limited. This perhaps explain decreased plant shoot height and number of branches at the later stage of the experiment under nutrient treatment. The findings provide evidence that all climate change scenarios tested promote the invasive *A. mearnsii* growth, but the effect trends are varied among the factors.

### 3.5.3. Effects of global change scenarios on plant biomass

Results of this experiment showed that total dry biomass of *A. mearnsii* was improved at high temperatures, low rainfall, and high rainfall treatments compared to high nitrogen and combined interaction (low and high rainfall) treatments in relation to the control. The experiment has shown that interacting the factors jointly does not always consistently aid in invasive *A. mearnsii* total dry biomass accumulation. For example, combined interaction (low and high rainfall) treatments led to less total dry biomass at the end of the experiment, in comparison to the control. This demonstrates that *A. mearnsii* total dry biomass is more sensitive to increased temperatures and rainfall amounts than under increased nitrogen and combined interaction (low and high rainfall) treatments. The reason for higher total dry biomass under increased temperature and rainfall treatments depends on the cardinal temperature represented as either minimum, maximum or optimum as summarized by (Hatfield *et al.* 2015, 2011). This agrees with the present study findings that the additional temperature of  $+2^{\circ}C$  is ideal optimum for the growth of *A. mearnsii*.

An increase in temperature does not necessarily mean an improvement in plant growth but results suggest that because of a balance in plant nutrients with temperature, it led to an improvement in plant growth and development (Sardans and Peñuelas, 2012). This is consistent with a theory of optimal allocation McCarthy and Equist (2007) as previously explained. This means that elevated warming predominantly plays a fundamental role in improving invasive alien species at the seedling growth stage (Sk lov et al. 2015). The reason for less total dry biomass in nitrogen and combined interaction (low and high rainfall) treatments is that the resources required by the plants were not most advantageous and balanced for seedling establishment stage since plant species require an essential balanced amount of soil nutrients including nitrogen required by plants in the form of nitrates for vigorous growth and development (Leghari et al. 2016). As a result, insufficient nitrogen causes reduced plant growth, chlorosis on plant leaves, and affect stem, and branches development (Magistad et al. 1945). Uptake and utilization of nitrogen by plants are dependent on other factors such as plant species type, age, traits and nutrient availability amounts (Leghari et al. 2016). All plant species require a balanced optimum amount of nitrogen fertilizer for its significant role of enhancing plant growth (Leghari et al. 2016). Ahmad et al. (2009) further emphasized by providing a strong evidence that depositing recommended optimum nitrogen fertilizer rates increases plant productivity,

photosynthetic performance, leaf production and the overall assimilation rates. However, numerous environmental factors such as soil, soil surface temperature, and climatic conditions behavior have a fundamental influence on the uptake and utilisation of nitrogen fertilizer (Leghari *et al.* 2016). Under favourable environmental factors the efficiency of nitrogen uptake and utilization becomes higher. Therefore, this provides an explanation that it is mandatory to consider the conditions before conducting an experimental study related to plant growth and development in response to nitrogen (Dong *et al.* 2015). An optimal partitioning theory by Zhang *et al.* (2019) states that plants should allocate more energy and nutrients to the parts that require the most limiting resources, this accounts for the present study findings of less total dry biomass under nitrogen and combined treatments (low and high rainfall). The recommended nitrogen fertilizer levels on the present study differed from other previous studies by (Song, 2017; Qiu *et al.* 2016). The study findings suggest that the growing environment has a fundamental influence on the plant response driven by climate change scenarios.

# 3.6. Conclusion

This study provides a demonstration of invasive A. mearnsii response to future climate change scenarios of elevated temperature, rainfall, soil nutrients, and combined interactions (low and high rainfall). Results demonstrate that increased temperature, rainfall, and soil nutrients exerts a significant improvement on seed germination and plant growth proportions specifically in terms of plant shoot height, number of branches, root length, and total dry biomass than the combined interactions. These findings support the hypothesis that under future elevated temperature, rainfall, and soil nutrients the growth and development of A. mearnsii may increase. Low rainfall amounts led to less seed germination and seedling establishment. Therefore, if future rainfall amounts decrease, the spread of A. mearnsii invasion may be reduced. However, normal and high rainfall amounts resulted in greater A. mearnsii seed germination rates, indicating that the plant takes the advantage of high rainfall events throughout the rainfall season, and this may aid the plant to invade more natural ecosystems (Duncan et al. 2019). This indicates that A. mearnsii will continue to spread rapidly with increased rainfall events. However, combined interactions (high temperature and high rainfall) showed higher effectiveness on seed germination than on seedling survival. In the context of the Intergovernmental Panel on Climate Change (2007) that predicted future elevated climate change scenarios tested on this study, results point to rapid invasiveness of A. mearnsii caused by high seed germination than seedling establishment, and survival. The findings of this study indicate that the future predicted climate change scenarios in the context of IPCC have the potential to enhance A. mearnsii germination thus make it more invasive. From these findings, it can be suggested that other invasive plants (with similar traits) might respond in the same way to future manipulated climate change scenarios considered in this study. These potential future changes associated with A. mearnsii germination and growth will potentially result in exacerbated biodiversity loss, ecological and

socioeconomic impacts as a consequence of future *A. mearnsii* invasion in South Africa Le Maitre *et al.* (2011). Therefore, the Working for Water programme (WfW) in partnership with other ecological restoration project initiatives must put more effort into managing and controlling *A. mearnsii* invasion to minimise its potential negative effects and restore natural vegetation.

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# Chapter 4: Effects of predicted future climate change scenarios on soil chemical properties following invasive *Acacia mearnsii* growth under greenhouse conditions.

# Abstract

The IPCC predicts global temperatures will increase by between 1.1°C and 6.4°C in the 21st century and rainfall patterns will be altered. An altered climate will influence invasive species growth, which in turn, can change soil processes and properties given linkages with the climatic system through nitrogen, carbon, and hydraulic cycles. Previous studies in South Africa have examined the effects of invasive Acacia mearnsii on ecosystem and biodiversity loss, but no studies have quantified the potential impacts of climate change scenarios on soil chemical properties underneath A. mearnsii growth. In this study, changes in soil chemical properties were examined after A. mearnsii growth under different experimental manipulated climate change scenarios of increased soil surface temperature (+2°C), increased rainfall (+3 mm), decreased rainfall (+0.75 mm), soil nutrients (10 g/m<sup>2</sup>), and their combined interaction. Soil chemical properties of soil pH and resistance, total nutrient concentration of Phosphorus, Nitrogen, and Carbon, and exchangeable cations of Potassium, Sodium, Calcium, and Magnesium were examined before and after A. mearnsii growth under greenhouse conditions. Findings show that soil pH was significantly (P < 0.001) higher underneath invasive A. mearnsii growth in different experimental manipulation than before the experiment. Soil resistance showed significantly (P < 0.001) varying results before and after the experimental treatments manipulation in each treatment. However, soil total P was significantly (P < 0,001) higher after the experiment than before whereas both total N and C showed significantly (P < 0.001) varying results before and after the experiment. Exchangeable cation of K showed significantly (P < 0,001) higher concentrations before than after the experiment. To the contrary, most climate change scenario treatments showed significantly (P < 0,001) lower exchangeable cation of Na than before the experiment. Similarly, both exchangeable cations of Ca and Mg before the experiment were significantly (P < 0.001) lower than their averages after the experimental manipulation. This study findings conclude that growth of invasive A. mearnsii under different climate change scenarios has the potential to impact soil chemical properties. This might be due to high intake and utilization rates of soil properties by invasive A. mearnsii for its successful growth and survival under extreme climate change scenarios tested in this study.

Key words: Invasive Acacia mearnsii · Soil chemical properties · Climate change scenarios

### 4.1. Introduction

Plant invasion is not only a major threat to biodiversity, ecosystems, and human wellbeing but also to the economy (Adhikari *et al.* 2019). Expanding plant invasion has unpredictable influence on soil physicochemical properties since it is associated with varying effects such as increase, decrease or neutral effects (Mamba *et al.* 2019). This process gradually regulates and improves the total nutrient concentration (e.g. P, N, C) pools due to highly invasive alien plants performance traits, for example, fitness, size, and growth (Castro-D ez *et al.* 2014; Liao, 2008; Van Kleunen, 2010). Available literature indicates that introduction of invasive alien plants can change soil properties compared to the effect is not always consistent since it depends on various factors such as invasion history, invasion extent, invasive plant species, season, recipient soil, habitat type and their interaction (Dasonville *et al.* 2008; Stefanowiez *et al.* 2016; Tharayil *et al.* 2013). However, in highly saturated riparian zones elevated soil nutrient levels may not be detected because of flood pulsing (Tererai *et al.* 2015).

Disturbance on soil physicochemical properties induced by plant invasion can either lead to enhanced or alleviated invasion (Stefanowiez et al. 2017). In addition, invasive alien plants severely alter important soil properties including total nutrient concentration of P, N, and C, pH, and fundamental exchangeable cations of K, Na, Ca, and Mg (Simba et al. 2013). Plant invasion is also seen as a fundamental process that improves the soil pH levels (Duda et al. 2003; Hughes et al. 2005; Vanderhoeven et al. 2006). In some cases, soil pH levels are significantly dependent on the degree at which the plant invasion is taking place. For example, low plant invasion extent leads to elevated soil pH than high plant invasion (Si et al. 2013; Wang et al. 2015). However, there are mixed findings among studies. Some studies have found that high plant invasion extent has the potential to significantly improve the levels of soil pH because they have high nitrate uptake and utilization rates that reduce nitrite concentrations in the soil, which in turn, leads to an increased soil pH (Ehrenfeld et al. 2001a, Fan et al. 2010, Si et al. 2013). Other studies reported that some invasive alien plants significantly improve soil pH levels but simultaneously creating detrimental effects on biodiversity (Milton et al. 1995). However, Ryan et al. (1983) reported contradictory findings that under Eucalyptus grandis stands soil pH levels decreases. In addition, some invasive grasses such as Microlaena stipiodes have been reported to increase their invasion extent with lower soil pH level requirements (Munnich et al. 1991). Invasive alien plants compete with native plants for limited soil properties such as nitrogen for successful invasion and biomass production (Chen et al. 2009; Laungani et al. 2009). Plant invasion also integrates with climate change since it is a principal driver for spreading invasive alien plants (Dullinger et al. 2017).

Climate change has severe impacts on soil physicochemical properties mostly induced and driven by various external factors such as elevated temperature, rainfall, and soil nutrient deposition (Anjali *et al.* 2019). Increasing soil surface warming has the potential to reduce organic matter in the soil through the combustion process (Ubeda *et al.* 2009). Certini (2005) argues that the organic matter reduction as caused by elevated temperatures leads to soil exchangeable cations reduction. In addition, Rengasamy and Churchman (1999) explains that atmospheric elevated warming increases the soil surface temperature that leads to a decrease in the soil exchangeable cations. However, Davidson and Janssens (2006), confirmed similar findings on low exchangeable cations as severely induced by leaching of cations because of extreme precipitation events.

Climate change scenarios are expected to have a severe impact on soil physicochemical properties due to fluctuations in temperature, rainfall, and nutrient deposition (Bard, 2017; French et al. 2009). Elevated soil surface warming has the potential to increase soil pH levels because of the organic acid denaturation that improves with elevated temperatures (Menzies and Gillman, 2003). Soil physicochemical properties will more likely change by either decreasing or increasing as predicted future climate change scenarios continue to worsen (Soriano-soto et al. 1995). Trenberth et al. (2007) observed that the interaction between the soil and changes in climatic factors such as rainfall and temperature can determine the soil processes that induce its physicochemical properties. As a result, it is very vital to evaluate and quantify how the soil interacts with variations of climate change scenarios (Gelybo et al. 2018). Yilvaiaio and Pettovuori (2012) observed that increasing soil surface warming from a range of 5 - 25°C has the potential to increase water-soluble phosphorus resulting in improved mobility of phosphorus in the soil. In this regard low soil surface temperature is associated with low phosphorus availability. Gahoonia and Nielsen (2003), explain that this is because low temperatures limits or hinders the release of the phosphorus from the organic matter and high temperatures allows the release of phosphorus from the decomposed matter in the soil. This study attempts to assess the impacts of climate change scenarios on soil chemical properties under different scenarios of climate change. Important basic soil chemical properties include soil pH, available total phosphorus, nitrogen, and carbon concentrations, and exchangeable cations of Mg, K, Ca, and Na, were selected because they are known to contribute to plant growth, thus potentially enhance alien plant invasion.

Soil pH is defined as the acidic and alkalinity of the soil normally ranging from 3 to 9. However, Lone *et al.* (2019) defined soil pH as the concentration of hydrogen ions found in the soil. Soil total nutrient concentrations (P, N, C) are fundamental soil chemical properties vital for plant growth and survival (He *et al.* 2012). Cation exchange is the total exchangeable cations that can be absorbed by the soil (Mamba *et al.* 2019). It indicates the capacity of the soil to absorb the soil nutrients (Ross *et al.* 2008).

Additionally, it is commonly referred to as the percentage basic cation saturation (Gelybo *et al.* 2018). A basic cation constitutes major four exchangeable cations of K, Na, Ca, and Mg (Patil *et al.* 2018).

To the best of our knowledge, no previous study has looked at the individual and interactive effects of experimentally manipulated climate change scenarios on soil chemical properties underneath the growth of woody invasive *A. mearnsii* in South Africa. However, (Ruwanza and Tshililo, 2018) only quantified the short-term soil and vegetation recovery after invasive *A. mearnsii* removal. Other studies that have attempted to quantify changes in soil nutrients after invasion e.g. Ruwanza and Shackleton (2016) who quantified the effects of *Lantana camara* invasion on soil properties, do not examine changes under future climate changing scenarios. Therefore, the focus for this chapter is examining whether climate change scenarios (elevated warming, precipitation, soil nutrient content, and their combined interaction) affect soil chemical properties underneath the growth of woody invasive *A. mearnsii*. The study used a before and after *A. mearnsii* technique to examine changes in soil properties under different climate change scenarios. The study is motivated by the need to quantify soil nutrient changes under future predicted climate change to provide useful invasive alien plant control and management insight and address the impacts of invasive plant on soil ecosystems.

# 4.2. Methods and materials

# 4.2.1. Experimental design

The collected soils (as described in chapter 3) were used in a greenhouse-based experiment where temperature, rainfall, and soil nutrients were manipulated to simulate future global climate change scenarios and *A. mearnsii* was planted and monitored from January to May. Soils (500 g in germination pots) with *A. mearnsii* seedlings were exposed to the following climate change scenarios (as described in chapter 3), (i) high-temperature treatment; (ii) high rainfall treatment; (iii) Low rainfall treatment; (iv) increased soil nutrients treatment; (v) a combination of increased temperature, high rainfall, and increased soil nutrient content treatment; (vi) a combination of increased temperature. After the seedlings of *A. mearnsii* were removed, soils were collected and tested for the above-mentioned soils nutrients. Due to financial limitations, three replicated soils were collected from each of the above-mentioned treatment pots.

#### 4.2.2. Soil nutrient measurements

Prior to and after the experiment, soil chemical properties for soils used in this experiment were analysed for: Soil pH, soil resistivity, total nutrient concentrations (P, N, and C), as well as exchangeable cations (K, Na, Ca, and Mg). The soil pH, a measure of acidity and alkalinity was

measured in 1:5 soil: KCl extracts (Rhoades, 1982), filtered and analysed by atomic absorption spectrometry (SP428; LECO Corporation). Soil resistance was measured using a resistivity meter in ohms. Soil total P was analyzed by using a Bray-II extract, as described by Bray and Krutz (1945), and the total N was analyzed by complete combustion using an elemental analyzer (Euro EA; Eurovector, Milan, Italy). Soil total C was determined by using a modified Walkley-Black method, as described by Chan *et al.* (2001). Exchangeable cations were extracted in a 1:10 ammonium acetate solution by using the centrifuge procedure following Thomas (1982), filtered, and analyzed by atomic absorption spectrometry (SP428; LECO Corporation, St. Joseph, Michigan, USA).

#### 4.2.3. Statistical analysis

All statistical analyses were performed using TIBCO Statistica version 13.5.0.17 (Software Inc, 2019). Proof of normality and homogeneity of variance were tested using Kolmogorov-Smirnov and Lilliefors test, respectively. Data were normally distributed. Comparisons of soil pH, resistivity, total nutrient concentrations (P, N, and C), and the exchangeable cations (K, Na, Ca, and Mg) before and after *A. mearnsii* planting under different climate change scenarios manipulation were analyzed using one-way ANOVA since data were collected once and given that the before treatment was not subjected to climate change scenarios. Tukey Unequal N HSD post hoc tests for homogeneous groups were performed to determine the differences between the samples.

#### 4.3. Results

# 4.3.1. Soil pH and resistance

The bulk of the soils collected were sandy (88%) and the remaining were loam (12%). The soils before the experiment were strongly acidic with an accumulated average pH of 4,10 ± 0,01. Soils in all climate change scenarios including control treatments underneath the growth of invasive *A. mearnsii* were neutral with an accumulated average soil pH ranging between 6,5 and 7,5. Soil pH levels before and after experimental manipulation treatments showed a significant difference (P < 0,001, Figure 4.1A), with pH being highest in the combined treatment receiving high rainfall. With respect to soil resistivity, the comparisons were statistically significant (P < 0,001) higher in the treatments that received nitrogen, and both combined treatments as compared to other treatments and the before experiment soils. Soils in the before treatment experiment had low soil resistivity levels 1063,33 ± 68,88 compared to both high nitrogen and combined treatments which were 1756,67 ± 138,60, 1536,67 ± 128,37 and 1836,67 ± 53,64 respectively. In general, all combined climate change scenario treatments showed a high resistivity trend. The combined treatment with low rainfall had an

average of  $1536,67 \pm 128,37$  soil resistivity whilst the combined treatment with high rainfall had average of  $1836,67 \pm 53,64$  (Figure 4.1B).



**Figure 4.** Results show (A) soil pH levels, and (B) soil resistance measured before and after climate change scenarios experimental manipulation. Bars represent the mean  $\pm$  SE and one-way ANOVA results are shown. Bars with different superscripts are significantly different at *P* < 0,001.

# 4.3.2. Soil total nutrient concentration (P, N, C)

Soil total P concentration was significantly higher in all the treatments after the experimental manipulation but with varying extents with respect to different treatment considered compared to before the experiment (Figure 5A). Before the experiment, soil total P concentration accumulated a minimum average of  $3,2 \pm 0,2$ . Across all treatments after the experiment, soil total P concentration were highest in combined treatments where both high and low rainfall was added. Both combined treatment with low rainfall and the combined treatment with high rainfall had soil P averages of  $160,33 \pm 18,68$  and  $106,8 \pm 49,41$  respectively (Figure 5A). Soil total N concentration were statistically significant (P < 0,001) across all treatments. Soil total N concentration was lower before the experiment with an average of  $0.12 \pm 0.01$  compared to high temperature treatment with an average of  $0.19 \pm 0.01$ . The combined treatment with low rainfall and the control were significantly higher than the before treatment. A lower total N in comparison to the before treatment was reported in low rainfall treatment  $(0,10 \pm 0,01)$  and combined treatment with high rainfall  $(0,11 \pm 0,01)$  (Figure 5B). In contrast, soil total C concentration comparisons were significantly (P < 0,001) higher before the experiment with an overall average of  $2.32 \pm 0.04$  compared to both low rainfall treatment (1.85 ± 0.09), high rainfall treatment  $(2.25 \pm 0.36)$  and followed by combined treatment with high rainfall (2.2  $\pm$  0,12). With respect to the remaining climate change scenarios treatments an increasing trend was evident when comparing soil total C concentration level before the experiment with after the experiment. In this case, high temperature treatment accumulated an average of  $3,13 \pm 0,13$ , high



nitrogen treatment with an average of  $2,69 \pm 0,05$ , combined treatment with low rainfall with an average  $3,1 \pm 0,08$  and control treatment with an average of  $2,72 \pm 0,31$  (Figure 5C).

Figure 5. Results show (A) total P concentration, (B) total N concentration, and (C) total C concentration measured before and after climate change scenarios experimental manipulation. Bars represent the mean  $\pm$  SE for each treatment and one-way ANOVA results are shown. Bars with different superscripts are significantly different at P < 0,001.

# 4.3.3. Exchangeable cations (K, Na, Ca, Mg)

The exchangeable cations of K were significantly (P < 0,001) higher before the experiment with an accumulated average of  $0,25 \pm 0,00$  compared to all other climate change treatment scenarios and the control. All the comparisons were statistically significant (Table 3). However, the exchangeable cations of Na were significantly (P < 0,001) lower before the experiment with an average of  $0,29 \pm 0,01$  compared to high temperature treatment with an average of  $0,39 \pm 0,04$ . Exchangeable cations of Na comparisons had lower averages in soils after the experiment than before experiment soils. In this case, the exchangeable cations of Na were significantly (P < 0,001) higher before the experiment with an average of  $0,29 \pm 0,01$  compared to both low rainfall treatment with an average of  $0,28 \pm 0,02$  and high rainfall treatment with an average of  $0,27 \pm 0,03$ , followed by high nitrogen treatment with an average of  $0,24 \pm 0,01$ , combined treatment with high rainfall with an average of  $0,25 \pm 0,01$  and then control treatment with an average of  $0,28 \pm 0,03$ . Moreover, the exchangeable cation of Na comparisons before and after the experiment in combined treatment with low rainfall showed a neutral effect with an equal average of  $0,29 \pm 0,01$ . All these comparisons were statistically significant (Table 3).

With respect to exchangeable cations of Ca and Mg, exchangeable cation of Ca before the experiment was significantly (P < 0,001) lower with an overall average of  $1,37 \pm 0,03$  which increased to  $4,57 \pm 0,28$  in high temperature treatment, followed by  $3,13 \pm 0,03$  in low rainfall treatment, then  $3,77 \pm 0,20$  in high rainfall treatment, further increased to  $5,6 \pm 0,21$  in high nitrogen treatment,  $7,5 \pm 0,51$  in combined treatment with low rainfall,  $6,17 \pm 0,12$  in combined treatment with high rainfall and  $4 \pm 0,47$  in the control treatment.

Similarly, exchangeable cations of Mg increased from  $0.92 \pm 0.01$  before the experiment to  $3.13 \pm 0.17$  in high temperature treatment, followed by  $2.1 \pm 0.00$  in low rainfall treatment, followed by  $2.27 \pm 0.32$  in high rainfall treatment,  $1.53 \pm 0.07$  in high nitrogen treatment,  $1.27 \pm 0.12$  in combined treatment with low rainfall,  $1.37 \pm 0.03$  in combined treatment with high rainfall and to an average of  $2.43 \pm 0.19$  in control treatment. All these comparisons were statistically significant (Table 3).

**Table 3.** Results show exchangeable cations (K, Na, Ca, Mg) measured before and after climate change scenarios experimental manipulation. Data are means  $\pm$  SE and one-way ANOVA results are shown. Different superscripts indicate statistically significantly different at P < 0.05.

Soil properties	Treatments								One-way ANOVA	
	Before	НТ	LR	HR	HN	CLR	CHR	С	<b>F-values</b>	P-values
K (cmol(+)/kg)	0,25	0,17	0,14	0,13	0,11	0,13	0,13	0,14	33,54	0,001
	±	±	±	±	±	±	±	±		
	0,01 <sup>a</sup>	0,01 ь	0,01 <sub>bc</sub>	0,01 c	0,01 c	0°	0°	0,01 <sub>bc</sub>		
Na (cmol(+)/kg)	0,29	0,39	0,28	0,27	0,24	0,29	0,25	0,28	4,51	0,001
	±	±	±	±	±	±	±	±		
	0,01 <sup> a b</sup>	0,04 ª	0,02 b	0,03 b	0,01 b	0,01 ª b	0,01 <sup>b</sup>	0,03 <sup>b</sup>		
Ca (cmol(+)/kg)	1,37	4,57	3,13	3,77	5,60	7,50	6,17	4	43,51	0,001
	±	±	±	±	±	±	±	±		
	0,03 <sup>d</sup>	0,28 ь	0,03 c	0,20 c	0,21 ь	0,51 ª	0,12 ª	0,47 <sup>b</sup>		
Mg (cmol(+)/kg)	0,92	3,13	2,10	2,27	1,53	1,27	1,37	2,43	23,43	0,001
	±	±	±	±	±	±	±	±		
	0,01°	0,17 ª	0,01 <sub>bcd</sub>	0,32 <sub>bc</sub>	0,07 <sub>cde</sub>	0,12 <sup>e</sup>	0,03 <sup>de</sup>	0,19ª b		

Letters are HT = High temperature, LR = Low rainfall, HR = High rainfall, HN = High nitrogen, CLR = Combined treatment (low rainfall), CHR = Combined treatment (high rainfall), C = Control

# 4.4. Discussion

Findings of this study showed a great variance in measured soil variables before and after the experimental climate change manipulations. It was evident that soils before the experiment exhibited lower average soil pH compared to soils after the experiment. In this study low soil pH average within acidic soils before the experiment could be explained by low microbiological activity taking place in

the soil, though this was not measured in this study. The study findings on soil pH concur with the findings by Fujii et al. (2014). This is because exchangeable cations increase with an increase of soil pH levels (Mamba et al. 2019). Low soil pH in strongly acidic soils before the experiment is driven by decomposition process (Fujii, 2014; Ruwanza and Dondofema, 2020). However, acidic soils hinder the plants to uptake and utilize soil nutrients proficiently (Hayakawa et al. 2013). In contrast, all climate change scenario treatments underneath the growth of invasive A. mearnsii showed elevated soil pH levels, consistent with findings elsewhere (Ehrenfeld et al. 2001b; Fan et al. 2010; Kuebbing et al. 2013; Sharma et al. 2007). A plausible explanation for the finding is that most invasive alien species are known to have high nitrogen nutrient uptake and utilization rates leading to elevated soil pH levels because high uptake and utilization of nitrogen nutrients is associated with elevated soil pH levels in most cases (Ehrenfeld et al. 2001a; Fan et al. 2010; Kuebbing et al. 2013). Soil resistivity showed a decreasing trend in high temperature and low rainfall treatments only whereas in most of the treatments considered after climate change scenario experimental manipulation an increasing trend was observed although individual treatments varied in extent when compared with the soil resistivity average before the experimental manipulation. Thus, this explains that extreme conditions such as high nitrogen, and combined treatment (low and high rainfall) integration strongly influence soils to become more resistant. Increased soil moisture because of high rainfall events makes the soil less compact leading to reduced soil resistivity (Ruwanza and Dondofema, 2020). This is confirmed in several previous studies that confirmed that high moisture supply makes soils less compact than low moisture which makes them dry and compact (Buli ksi et al. 2014; Dantas et al. 2020).

An increasing trend of soil total P concentration was observed in all treatments after the experimental manipulation, but with varying extents with respect to each treatment considered compared to before the experiment. Varying soil total P concentrations were reported on previous study underneath the growth of different invasive alien species, for example soil total P was higher in soils invaded by invasive *Solidago gigantea* and *Impatiens glandulifera* (Chapuis-Lardy *et al.* 2006; Ruckli *et al.* 2014). Hou *et al.* (2018) reported that temperature, rainfall, and biological processes such as mineralization have significantly contrasting control on soil total P concentration availability in the soil. Fisher and Binkley (2000) state that soil total P concentration is limited in acidic soils. However, low soil total P concentration before the experiment could be associated with acidic soil as already stated. This was also evident in this study since soils before the experiment were strongly acidic. But that consistent trend was not observed in total nutrient concentrations (N and C) since they showed varying results before and after the experiment, respectively. This might have been driven by extreme conditions such as high rainfall that led to severe nutrient leaching also known as nutrient mobility throughout the experiment that occurred during watering (Kumar and Swarup, 2012; Weil and

Magdoff, 2004). Consequently, some soil total nutrient concentrations could have been lost during the process.

Similarly, soil C was higher in soils before the experiment compared to soils after the experiment in low rainfall treatment, high rainfall treatment, and combined treatment (high rainfall) except in other climate change treatments underneath the growth of invasive A. mearnsii. Decreased soil C in low rainfall treatment, high rainfall treatment, and combined treatment (high rainfall) is explained because of severe loss of soils caused by soil erosion due to intensive rainfall events (Xue et al. 2011). However, the soil N before and after the experiment showed varying results in different treatments considered. For example, it was higher before the experiment compared to after the experiment in low and high rainfall treatment, except in high temperature, rainfall, nitrogen, combined treatment (high rainfall), and control treatments. Varied effects of climate change scenarios under plant invasion on soil chemical properties in this study could be explained by various factors such as plant species. For example, Kerr and Ruwanza (2015) reported elevated soil pH, total P concentration and decreasing total nutrient concentration of N and C underneath the growth of invasive Eucalyptus grandis. Findings of decreased soil N in low rainfall and combined treatment with high rainfall could be attributed to waterlogging conditions that might have occurred in those treatments throughout the experiment, consistent with findings by Moran et al. (2000). Other findings have revealed that low nitrogen availability is associated with native species than invasive alien species (Laungani et al. 2009).

Invasive alien species uptake and utilize excessive nitrogen nutrients to achieve their maximum growth, competitive ability, and invasion extent (Maztek, 2011; Ochoa-Hueso, 2011; Wang *et al.* 2014). However, higher soil N trend in climate change treatments underneath the growth of invasive *A. mearnsii* compared to soils before the experiment could be as result of nitrogen fixation by invasive *A. mearnsii*. Laungani *et al.* (2009) show that high nitrogen availability favours invasive alien species than native species. Common invasive alien species such as *Acacias, Eucalyptus* and *Lantana* have been shown to elevate soil total nutrient concentrations (Ruwanza *et al.* 2013). This is also consistent with findings by Osunkoya *et al.* (2005) and Morris *et al.* (2011) who reported the same abovementioned trends. *Acacia mearnsii* is known to be a good leguminous nitrogen fixer (Krisnawati *et al.* 2011; Moyo and Fantubi, 2010). In this study, the soils were planted with invasive *A. mearnsii* from November 2019 and harvested in May 2020, so it is not surprising that soil N was higher after the experimental manipulations compared to before the experiment. So indeed, competitive *A. mearnsii* invasion favoured and improved some soil physicochemical properties, for example soil N, for its growth (Wang *et al.* 2011). The decreasing trend in nutrient consumption by invasive *A. mearnsii*, as has

been found elsewhere (Feng *et al.* 2007). However, some soil nutrient concentrations are exacerbated by various external factors, including severe soil erosion and nutrient leaching (Shen and Hong, 2003).

In the context of climate change scenarios, intensive rainfall events facilitate nutrient leaching and mobility (Moran et al. 2000; Patil et al. 2018; Xiong et al. 2008). Exchangeable cation of K showed an increased trend only before the experimental manipulation compared to its averages in all the climate change scenarios. The exchangeable cation of Na average was higher in soils before the experiment compared to soils after the experiment except in combined treatment with low rainfall soils underneath the growth of invasive A. mearnsii. In this study, it was evident that soils under climate change scenario treatments after the experiment underneath the growth of invasive A. mearnsii had significantly higher exchangeable cation of Ca average compared to soils before the experiment. This is because of the fast-growing leguminous, nitrogen-fixing invasive A. mearnsii that uptake and utilize higher exchangeable cation of Ca proportions for various purposes on its life cycle for example, for plant biomass accumulation. This finding has also been highlighted by Yamashita et al. (2008). In this present study it can be attributed to less uptake and sequestration of exchangeable cation of Mg underneath the growth of invasive A. mearnsii. Contrary, the present study does not concur with the previous findings by Hagar et al. (1991), who found contradictory findings of lower exchangeable cation of Mg due to higher uptake and sequestration by invasive Acacia plants. Changes in soil physicochemical properties after the experiment are driven by different external factors such as temperature, rainfall, nutrients, and plant invasion (Cuesta et al. 2012). Previous study findings have shown that extreme environmental conditions such as high rainfall events are associated with high degree of plant invasion (Chytry et al. 2008; Huebner et al. 2006).

# 4.5. Conclusion

This study concludes that climate change scenarios of increased temperature, rainfall, soil nutrients, and their combined interaction treatments (low and high rainfall) have the potential to alter and persuade most soil chemical properties that can enhance *A. mearnsii* growth. This is because most invasive alien plants such as the invasive *A. mearnsii*, succeed with the prominent impact they induce on soil physicochemical properties under climate change scenarios (Sardans *et al.* 2017). However, changes in soil chemical properties play a significant role on the growth and survival of invasive plants through creating suitable, favorable, and adaptable growth conditions (Ruwanza and Dondofema, 2020). There is strong evidence in this present study that suggests invasive *A. mearnsii* significantly increase the soil pH levels with varying climate change scenarios. This is evident when comparing the soil chemical properties levels before and after the experimental manipulation. But the soil effect varies between different climate change scenario treatments that were considered. In some

cases, soil chemical properties decreased, and in other cases increased in comparison to the averages before and after the experiment, consistent with findings reported by Stefanowiez *et al.* (2017) and Lone *et al.* (2019). The observed trends will continue to increase since climate change and plant invasion are predicted to worsen in the future decades due to several factors e.g.  $CO_2$  increased and globalization (Liao *et al.* 2008). These findings can aid in understanding the effects of climate change scenarios with expanding plant invasion. For example, understanding changes in soil chemical properties induced by climate change and plant invasion may contribute to the development of new techniques of manipulating soils in ways that prevent and reduce alien plant invasion (Bulot *et al.* 2017; Wubs *et al.* 2016).

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## **Chapter 5: Conclusions and future research recommendations**

#### 5.1. Key research conclusions

This thesis reports on the effects of predicted future climate change scenarios on the germination and growth trends of invasive *Acacia mearnsii*, and on soil chemical properties under greenhouse conditions. The different climate change scenarios examined in this study are (i) elevated soil surface temperature ( $+2^{\circ}$ C), (ii) increased (+3 mm) and decreased (+0.75 mm) rainfall, (iii) increased soil nutrient content (10 g/m<sup>2</sup>), and (iv) their combined interactions in a pot and microcosm experimental system. The study is motivated by the need to gather information on invasive *A. mearnsii* response to future climatic changes and quantify soil nutrient changes under future predicted climate change. The main conclusions are as follows:

- 1. The study findings indicate that germination of invasive A. mearnsii tolerates individual climate change scenario treatments. This result from excess resources supplied to the soil, favourable for successful seed germination by increased climate change scenarios, but to some extent low rainfall reduces seed germination due to soil surface drying because of low water content available on the soil. The integration of different climate change scenarios and treatments did not have the synergistic effects on the optimum seed germination. It is possible that high germination under future climate change scenarios can aid A. mearnsii to more likely spread and flourish on over a short period and increase its invasion extent (DWAF, 1997; Henderson, 2001). It is evident that small changes, even in rainfall events, such as low rainfall have a limited influence since plant germination and growth showed a limited response, consistent with findings by Gerten et al. (2008) and by Miranda et al. (2009). The findings also suggest that low rainfall events can extremely limit and hinder seed germination (Dantas et al. 2020). A developed hierarchy of ecological response to rainfall events indicate that the impact of rainfall on plant growth ranges from hours to decades (Schwinning et al. 2014). Consequently, it is fundamental to understand how plants species respond to changes in rainfall events (Beier et al. 2012; Reyer et al. 2012). Experimental studies have highlighted that in some cases, elevating rainfall events over a short-term has the potential to facilitate long-term plant invasion establishment (Dukes et al. 1999). This indicates that initial changes induced on climate change scenarios might push invasive A. mearnsii plant community to a new threshold and facilitate its invasion.
- 2. The study findings demonstrate that plant shoot height of *A. mearnsii* responds positively to increased individual and integrated manipulated climate change scenario treatments, but with varying seedling growth extents observed for each treatment. Therefore, the findings suggest that climate change scenarios have the potential to give rise to fast *A. mearnsii* plant growth. Enhanced warming has been shown in previous studies conducted on plant growth to be

mainly effective on plant phenology changes (Thuiller *et al.* 2007). As climate is predicted to continue to change further in the upcoming decades, rapid plant invasion will be more facilitated by changes in plant physiology. From the above-mentioned invasive *A. mearnsii* growth potential, it can be predicted that there will be enhanced growth that is likely to cause severe socioeconomic and ecological effects associated with the unabated continuous invasion by *A. mearnsii* (Yapi, 2013). Climate change scenarios were found to exacerbate the success of invasion by *A. mearnsii* by contributing to its high growth rate and size traits e.g. explored plant shoot heights.

- 3. Reduced rainfall, increased nitrogen nutrients and a combined treatment with added rainfall were found to favour the growth of invasive *A. mearnsii* seedlings, due to significant increase in the number of branches developing than combined treatment with added low rainfall treatment which did not have a profound effect on the seedlings to develop more branches. From these observed trends it is clear that rainfall changes e.g. extreme and reduced rainfall have inconsistent effects on plant growth traits e.g. number of branches (Zeppel *et al.* 2014). This is because extreme rainfall is associated with wet conditions whereas reduced rainfall is associated with water deficit conditions. This study brings us to a closer understanding that the individual effect of enhanced rainfall is driven by integration between various factors such as plant available water, plant functional type, plant phenology, and growth (Zeppel *et al.* 2014). Elevated nitrogen deposition to the soil is observed to create an adaptable condition and transforming potential for fast growing non-native plants e.g. invasive *A. mearnsii* (Berendse *et al.* 1993).
- 4. This study findings suggest that invasive *A. mearnsti* seedlings growing under individual treatments are highly competitive and this leads to longer root lengths spreading in the soil than under integrated treatments that seem to have less effect on seedling root length growth. It is common to observe varied trends e.g. increases, decreases and no change effects in some circumstances under altered climate change scenarios (temperature, rainfall, and nitrogen nutrients) regimes (Bradley *et al.* 2010; Dukes *et al.* 1999). Following the climate change scenario projections, more marked changes on plant productivity trait e.g. root length can be expected. Plant roots are mainly significant for up taking water and soil nutrients but climate change scenarios such as soil surface temperature can disrupt those processes, which may result in limited plant growth in some circumstances (Calleja-Cabrera *et al.* 2020). With these given predicted climate change scenarios efficient root system developed by plants is required for facilitating crucial plant productivity. Plant water demands worsen as temperatures gets warmer, as a result of evapotranspiration and excessive water acquisition by roots to meet the plant water requirements (Heckathorn *et al.* 2013).

- 5. Invasive A. mearnsii seedlings growing under elevated individual climate change scenarios significantly enhance the plant's total dry biomass than combined treatments. This was observed on the study findings that individual climate change scenario treatments accumulated high total dry biomass than integrated treatments. This might be because seedlings under individual treatments grew faster than seedlings under integrated treatments. In addition, invasive A. mearnsii species is commonly known to have high biomass accumulation trait (Yapi, 2013). Available literature highlights that plant biomass can either increase or decrease depending on soil water content respectively e.g. elevated or decreased soil water content driven by rainfall events (Zeppel et al. 2014).
- 6. This study showed that elevating climate change scenarios and introducing invasive A. mearnsii significantly give rise to soil pH levels making the soil to be more acidic. Soil resistivity responds differently to different climate change scenarios. For example, soils with increased nitrogen nutrients, and combined treatments with reduced and added rainfall amounts increase the resistivity of the soil than under individual rainfall and temperature events. All climate change scenarios improved soil total P concentrations. Exposing soils to increased temperature, nitrogen, and combined treatment with low rainfall were found to improve soil total N concentration. However, increasing rainfall and combined treatment with high rainfall were found to reduce soil total N concentration. Under enhanced soil surface temperature and combined treatment with low rainfall soil total C concentration were found to increase. In general, rainfall, nitrogen, and a combined treatment with added rainfall were found not to have a significant impact on soil total C concentration. Yapi (2013) explored that A. mearnsii invasion improves the soil pH, concentrations of soil P, N, and C. However, exchangeable cation of K, Na, Ca, and Mg are severely affected by climate change scenarios with the introduction of invasive A. mearnsii to the soil, but each treatment effect varies in extent to another. Consistently, (Ruwanza and Dondofema, 2020) highlighted that some invasive plants e.g. guava plant influences soil properties e.g. by increasing soil total P concentration and other soil physical properties e.g. soil moisture and infiltration rate. The study findings indicate that changes observed in soil chemical properties considered could enhance the growth and facilitate the flourishing of A. mearnsii invasion.

# 5.2. Recommendations

The growing trends of invasive *A. mearnsii* seedlings when exposed to future predicted climate change scenarios (temperature, rainfall, and soil nutrients) indicate that plant invasion induced by climate change is more likely to worsen in the nearby future. Following the findings of this study, it can be recommended that conservation organizations must put more effort on the control and management of invasive *A. mearnsii* and other known problematic invasive alien plants in South
Africa in order to save biodiversity resources. This recommendation follows the observed potential future changes in growth responses of *A. mearnsii* associated with climate change scenarios in this study. This study's findings concur with the previous findings by Jia *et al.* (2016) who reported that environmental change induced by climate change promotes the growth of invasive alien plants, mostly through plant growth rate and size traits. Quantifying the response of invasive alien plants to climate change can easily indicate a possible plant niche that can help in understanding the current, future spread and distribution patterns of invasive alien plants (O'Brien *et al.* 2013).

In some cases, for example under low rainfall conditions there is a limited effect on seed germination since it slowed the germination percentage most probably induced by soil surface dryness, indicating that rainfall supplied to the soil is insufficient to trigger germination. However, nitrogen accumulation by the plants has a close relationship with the amount of the nutrients supplied to the soil (Chen et al. 2014). So, this study recommended that nitrogen must be managed properly for right methods and quantity application before any soil tests that might interfere with the quality of the soil. This highlights that the variability, distribution, size, and particular timing of certain climate change scenarios such as individual enhanced rainfall and nutrients have strong influence on plant growth compared to the unaltered conditions (Heisler-White et al. 2008, 2009; Reyer et al. 2012; Smith, 2011; Schwinning et al. 2004; Thompson et al. 2013; Zeppel et al. 2008). But in some circumstances, the influence depends on the environment, for example, it has been shown that natural forests alter and induce fluctuations for their own certain conducive temperature and rainfall conditions (Bonan, 2008). Quantifying the impacts of climate change on soil chemical properties is important for understanding how soil chemistry is affected following the alterations induced by climate change (Asit et al. 2012). From a management point of view, controlling invasive A. mearnsii on natural ecosystems is encouraged to reduce its severe impacts on both native vegetation and soil physicochemical properties levels. Future research must develop feasible and appropriate invasive A. mearnsii managing methods that can be implemented following its growth trends and impacts on soil chemical properties determined and given in this study. A key recommendation is that the future control of A. mearnsii should be accompanied by measures to improve soil nutrients that might have been reduced by the invasive plant. Indeed, Nsikani et al. (2017) reported that soil legacy effects caused by invasive alien plants like Acacias (in this above-mentioned study A. Saligna) can last for more than 10 years after the plant's removal. Therefore, there is a need to further investigate changes in soils during and after plant invasion.

It is recommended that future research on biological invasion should investigate changes in both plant behavior and soils under different future scenarios. This will provide a useful insight and help to understand and plan how, when, and where the management plan for invasive alien plants can be implemented. Future research on climate change and plant invasion should also recognize the scenarios considered in this study but on different problematic invasive alien plants, e.g. *Lantana*, *Pinus*, and *Eucalyptus* which are known to be problematic plants in South Africa. This could provide a broader insight on the impacts of different climate change scenarios on invasive alien plant behaviour. Exploring the invasion extent of *A. mearnsii* exacerbated by climate change scenarios demonstrated in this study will also help to guide its control and management plans to suppress its impacts on soil, water, and vegetation biodiversity in South Africa (Le Maitre *et al.* 2000). Finally, more studies on manipulated future climate change predictions must be conducted to fill the knowledge gap and address its effects on plant diversity.

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