Dynamics of a flammable species in a forest landscape: A case study on forest wiregrass *Tetrarrhena juncea* R.Br.

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Doctor of Philosophy
March 2022
Faculty of Science
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Submitted in total fulfilment for the degree of
Doctor of Philosophy
at the University of Melbourne

Abstract

Species abundance often determines the extent of influence of a species to ecosystem function and processes. Typically, the abundance of a species is constrained by environmental factors within its habitat. However, there are instances where native species becomes prolific and the shift in abundance greatly impacts the ecosystem. Such is the case when a flammable species becomes prolific within its range and alters the flammability of the ecosystem. This is a concern with climate change, as conditions might be tipped in favour of such species. Hence, it is crucial to understand the drivers of abundance to understand how native species can be released from environmental constraints of abundance to become prolific within their own range, and to predict the potential effect of changing environmental conditions on their abundance. Thus, the overarching aim of this thesis was to understand how a flammable native species can become prolific within its own range. This is achieved using a case study species – forest wiregrass *Tetrarrhena juncea* R.Br. (hereafter *wiregrass*) – an understorey native species that is of high importance to flammability in the eucalypts forests of south-eastern Australia and grows prolifically under certain conditions.

The overarching aim of the thesis was addressed using a mix of research methods to identify the key drivers of wiregrass distribution and abundance. Firstly, a database of the current distribution for wiregrass were analysed using species distribution modelling to identify highly suitable habitat for wiregrass (Chapter 2). Temperature seasonality, precipitation of the driest month, rainfall seasonality, annual mean temperature, the minimum temperature of the coldest month and soil pH were strongly associated with the suitable habitat of wiregrass. The high importance of climatic factors indicates the distribution of wiregrass may be sensitive to climate change. Highly suitable habitats do not necessarily harbor abundant wiregrass because site-specific factors can also control abundance. Hence, Chapter 3 sought to identify the factors most important to wiregrass abundance in the highly suitable habitat of Mountain Ash-dominated forest. Wiregrass cover was assessed in a field survey across a chrono-sequence of 126 sites with contrasting disturbance histories. Canopy cover and net solar radiation were the most important predictors of wiregrass abundance, with wiregrass cover highest in recently disturbed areas with sparse canopy cover, high light levels, and low precipitation. The final component of the thesis used a glasshouse experiment to quantify causal links between resource availability and wiregrass abundance. Wiregrass growth was more sensitive to water availability than light, whereas biomass allocation and leaf morphology were more sensitive to light availability.

Collectively, the results showed that, where wiregrass is present (distribution), three key conditions will greatly favour its prolific growth (abundance): (i) non-limiting water resource; (ii) reduced canopy cover and increased light; and (iii) recent disturbance. These key results strongly suggest wiregrass can become prolific when resources are increased, and the vegetation community is substantially disturbed. Under such conditions, increased wiregrass abundance could create a window of increased flammability for the forest ecosystem. Since climate change can alter resource availability and disturbance regime, shifts in wiregrass abundance are likely to occur under future climate scenarios.

Declaration

This is to certify that:

i. the thesis contains only my original work towards the Doctor of Philosophy except where indicated in the preface;

ii. due acknowledgment has been made in the text to all other material used;

iii. the thesis is fewer than 100,000-word limit in length, exclusive of tables, maps, bibliographies and appendices.

(Signed)

Geofe O. Cadiz

Preface

This thesis contains five chapters – a general introduction, three data chapters, and a general discussion. The three data chapters are written in article format with the following publication status and details:

Chapter 2 – unpublished material not yet submitted for publication.

Chapter 3 – published by Australian Journal of Botany on 7th May 2020.

> Cadiz, G.O., Cawson, J.G., Penman, T.D., York, A., and Duff, T.J. 2020. Environmental factors associated with the abundance of forest wiregrass *(Tetrarrhena juncea)*, a flammable understorey grass in productive forests. Australian Journal of Botany 68:37-48. https://doi.org/10.1071/BT19112
>
> *Author contributions:*
> Cadiz, G.O. – primary author; carried out the research, analysed and interpreted the data, and drafted the manuscript.
> Duff, T.J. – contributed to the interpretation of data.
> Duff, T.J. and Cawson, J.G. – acquired funding and resources for the study.
> All authors reviewed, edited, and approved the manuscript.

Chapter 4 – published by Plant Ecology on 11th June 2021.

> Cadiz, G.O., Cawson, J.G., Duff, T.J., Penman, T.D., York, A., Farrell, C. 2021. Independent effects of drought and shade on growth, biomass allocation and leaf morphology of a flammable perennial grass *Tetrarrhena juncea* R.Br. Plant Ecology 222: 877–895. https://doi.org/10.1007/s11258-021-01148-y

Author contributions:

Cadiz, G.O. – primary author; carried out the research, acquired funding and resources for the study, analysed and interpreted the data, and drafted the manuscript.

Farrell, C. and Duff, T.J. – contributed to the interpretation of data.

Duff, T.J. and Cawson, J.G. – acquired funding and resources for the study.

All authors reviewed, edited, and approved the manuscript.

I would like to gratefully acknowledge the sources of funding towards my PhD:

a. *Melbourne International Research Scholarship;*
b. *Melbourne International Fee Remission Scholarship;*
c. *Department of Environment, Land, Water and Planning* (DELWP) through the research project ‘‘Managing bushfire in Tall Mist Forests—fuel hazard and moisture relationships.’’ This project was managed within the Integrated Forest Ecosystem Research program, a research program conducted by the University of Melbourne and funded by DELWP;
d. *Research Higher Degree (RHD) Student Research Accelerator Fund* of the School of Ecosystem and Forest Sciences (SEFS) of the University of Melbourne, Australia; and
e. *Doctoral Fellowship* of the University of the Philippines.

Acknowledgments

I would first like to thank my supervisors whose untiring guidance, invaluable advice, and support have tremendously helped me navigate through my PhD journey and complete my thesis. I am deeply grateful to Dr. Jane Cawson for her conscientious mentorship and help from the conceptualization of the thesis to the proofreading of the final manuscript; to Dr. Thomas Duff for his insightful comments and suggestions on every part of the thesis, and for actively sourcing out support funding; to Prof. Trent Penman for helping me with the species distribution modelling and the write-up structure; and to Prof. Alan York for his helpful feedback, advice, and administrative help. I also appreciate them all greatly for their careful review of manuscript drafts.

I would like to express my special thanks to Dr. Claire Farrell for her invaluable help and expert guidance in my glasshouse experiment, and carefully reviewing the corresponding manuscript draft for publication. Many thanks also to my advisory committee – A/Prof. Craig Nitschke, Dr. Claire Farrell, Dr. Rebecca Miller and Dr. Matthew Bruce – for the assistance they provided over the course of my studies.

I would like to extend my sincere thanks to Mr. Simon Murphy, Dr. April Gloury, Dr. Tom Fairman, Dr. Naomi Davis and Mr. Peter Mercouriou for their assistance with field data collection, and Dr. Matthew Swan for his help in site selection; Craig Baillie and Anna Maria Magda Demeterio for their assistance in the collection of wiregrass planting materials; Nicholas Osborne and Rowan Berry for preparing and maintaining the glasshouse, securing the needed materials for the experiment, and administering pesticides; Radames Gaspar Santos Anacleto for his help in wiregrass propagation; Dr. Chris Szota, Dr. Carola Pritzkow and Dr. Brisneve Edullantes for their technical help; Jane Paula Cruz, Melody Palbusa, and Karisse Perey for their help in the harvest process; and the handling editors and anonymous reviewers of the two published chapters for their careful review and invaluable comments to improve the manuscripts. I also greatly appreciate Dr. Claire Farrell and Dr. Rebecca Miller for giving me emotional support, affirmation, and encouragement.

To my Creator and Redeemer, the Almighty God, for the countless blessings and sustaining grace throughout my PhD journey, I am forever grateful.

Daghang salamat!

Table of Contents

Page

List of Tables

List of Figures

Page

1 General Introduction

PROBLEM STATEMENT AND AIM

Vegetation as wildfire fuel

Vegetation is the fuel for wildfires and therefore the properties of plant species making up vegetation communities influence landscape flammability (Murphy *et al.* 2013; Zylstra *et al.* 2016; Duff *et al.* 2017). Plants that have the greatest influence on the flammability of a plant community are those that are dominant or exhibit highly flammable traits. Dominant species strongly influence the flammability of a vegetation community by playing a key role in defining the total fuel load, and the physical and chemical properties of the fuel bed (Schwilk and Caprio 2011; Tumino *et al.* 2019). Species with highly flammable traits can disproportionately influence the flammability of a species mix, when two or more species burn together (Wyse *et al.* 2017). Species that are both dominant and highly flammable could influence the fire regime (i.e. intensity, frequency, extent, type, seasonality) of a system (Brooks *et al.* 2004). Shifts in the distribution and abundance of flammable species could change the flammability of the whole plant community (Gill and Zylstra 2005; Simmons *et al.* 2006; Zylstra 2011; Schwilk and Caprio 2011; Duff *et al.* 2017). Therefore, it is important to understand how flammable species respond to current environmental factors and future changes in climate. Yet, for many such species this understanding is lacking.

Patterns of plant distribution and abundance

A primary goal of macroecology is to identify and understand patterns in natural systems, and the influence of disturbances and environmental change to these patterns. This goal is particularly significant in the face of climate change and altered disturbance regimes. It would be difficult to predict how species would behave under future climate and disturbance without an understanding of these patterns in nature. Patterns of species distribution (where species occur) and abundance (where species thrive in numbers or biomass) are two patterns that have received much attention in studies on the effects of climate change (Fowbert and Lewis Smith 1994; Smith 1994; Hughes 2000; Parmesan 2006; Bertrand *et al.* 2011; Chen *et al.* 2011; Doxford and Freckleton 2012; Gottfried *et al.* 2012; Zhu *et al.* 2012; Telwala *et al.* 2013; Settele *et al.* 2015; Lenoir and Svenning 2015; Kosanic *et al.* 2018).

Understanding the factors that drive species distribution is important as species occurrence is a necessary precursor to abundance. However, the relationship between plant occurrence and abundance (abundance-occupancy relationship or AOR) is not always positive (Thompson *et al.* 1998; Riis and Sand-Jensen 2002; Heino and Virtanen 2006; Kolb *et al.* 2006; Buckley and Freckleton 2010; Duff *et al.* 2011). In other words, the high probability of species occurrence does not necessarily correspond to high probability of abundance because environmental factors can exert differential influence on occupancy and abundance (Duff *et al.* 2011). Since the influence of a species within an ecosystem (e.g. its contribution to ecosystem flammability) is often proportional to its abundance (Radford *et al.* 2005; Baeza *et al.* 2006; Fernandes 2009; Bradley 2016), it is important to know when and where it is likely to become abundant. This requires an understanding of the influence of environmental factors on distribution and abundance.

Generally, atypical abundance of native species is constrained by biotic interactions in its community. Pulses of increased abundance may happen for pioneer species after disturbances but tend to reverse following succession (Odum 1969). However, some native species show unusually high abundance or biomass that persist for several years or decades consistent with exotic invasive species or weeds (de la Cretaz and Kelty 1999; Simberloff *et al.* 2012; Pivello *et al.* 2018). Such native species are referred to as *super-dominant* (Pivello *et al.* 2018), *overabundant* (Jose *et al.* 2016), *weeds* (Richardson *et al.* 2000), or *native-invasives* (Valéry *et al.* 2008, 2013). Their persistence at unusually high levels of abundance suggests they are released from natural constraints to their high abundance. Hence, understanding how a native species can become prolific within its own range can help us understand how native species can be released from environmental constraints to their abundance to become potentially weedy. Central to this is identifying the factors or conditions that cause an increase in abundance – if these factors or conditions persist for a long time, high abundance might also persist for a long time. These environmental drivers of high abundance are poorly understood across most species. This is an important knowledge gap in the face of climate change because future climate conditions may give a relative advantage to some native species to rapidly increase in distribution and abundance.

Key concepts underpinning patterns of plant growth, distribution, and abundance

Established theories and concepts can help explain the patterns of plant distribution and abundance in natural systems. These patterns are a function of the interaction of the species with its abiotic and biotic environment (Figure 1.1). The abiotic environment consists of climatic, edaphic, resource and topographic factors, while the biotic environment includes interactions with other species such as herbivory, pest infestation/parasitism, intra- and interspecific competition, or demographic changes within population. These abiotic and biotic factors can vary in space and time. Furthermore, the abiotic and biotic environment are often interconnected – plant species can alter the abiotic environmental conditions (e.g. tree canopies can influence microclimatic conditions beneath the forest canopy), and abiotic factors can influence species interactions (e.g. limited resources can increase species competitions).

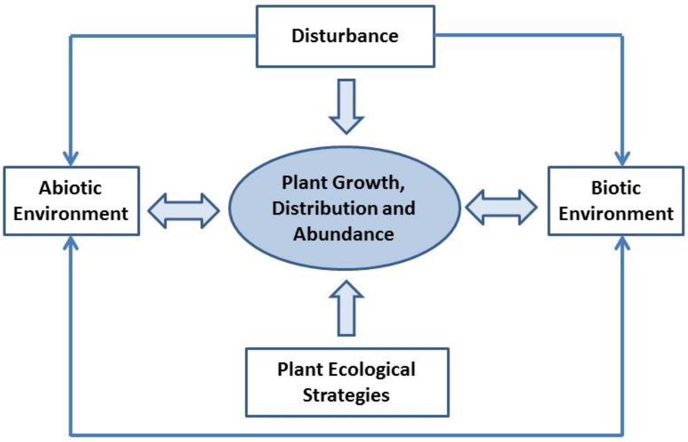


Figure 1.1 Plant growth, distribution and abundance are reflections of plant's ecological strategies acting within the context of the biophysical environment, which can be modified by disturbance.

These patterns of plant distribution and abundance as affected by the biophysical environment is intimately associated with the niche of the species. The species fundamental niche is a specific set of abiotic and biotic conditions and resources in which the species could survive and reproduce (Grinnell 1917; Hutchinson 1957; Vandermeer 1972; Brown 1984; Hall *et al.* 1992; Hirzel and Le Lay 2008). This fundamental niche determines the suitable habitat (Kellner *et al.* 1992; Hirzel and Le Lay 2008) where species can be found (distribution or occupancy) and where it thrives in numbers or biomass (abundance or dominance). However, in the presence of other organisms interacting and competing for the available resources, species can only occupy a narrow portion of their fundamental niche, called the realized niche (Hutchinson 1957).

A. Plant ecological strategies

Plants have genetically determined functional traits and mechanisms that allow them to respond to the environment to survive, reproduce, defend, and compete in the landscape. These intrinsic functional traits and mechanisms allow plants to make trade-offs in responding to their environment. For example, plants under shade will invest more biomass in leaves (increased leaf mass fraction, leaf area, leaf area ratio and specific leaf area) to enhance light capture (Loach 1967; Aerts *et al.* 1991; Lambers *et al.* 2008) at the expense of reduced allocation to roots (Smith and Huston 1989). Conversely, plants under dry conditions will invest more biomass in roots (increased root mass fraction) to enhance water absorption (Evans 1972; Aerts *et al.* 1991; Poorter *et al.* 2012) at the expense of reduced allocation to leaves (Smith and Huston 1989). These trade-offs are argued to be the consequence of the trade-off in phenotypic adjustment of functional traits (traits in parentheses in the preceding sentences) under changing resource availability (Chapin *et al.* 1987; Smith and Huston 1989; Valladares *et al.* 2007; Couso and Fernández 2012) and can explain the ability of plants to grow and survive when resources become limiting (Bradshaw 1965; Sultan 2000; Nicotra *et al.* 2010; Amissah *et al.* 2015).

Based on these functional traits and mechanisms, plants can be classified into different ecological strategies according to how they respond under varying levels of competition, stress, and disturbance – competitors, stress tolerators, ruderals, and combinations of the first three (Grime's C-S-R Triangle) (Grime 1977; Pierce *et al.* 2017). Each plant species has strategies that show resource trade-offs between growth, reproduction, and maintenance in response to two factor gradients, stress and disturbance (Grime 1977), which vary across space and time. Grime (1977) enumerated stress factors to include reduced resource availability (water, light, nutrients), non-optimal temperatures, or presence of toxins (e.g. heavy metals in soil); forms of disturbance include fire, human activities (e.g. logging, mowing), windstorms, or flood. Stress and disturbance can limit plant biomass, consequently influencing growth, distribution, and abundance.

Plant growth, distribution and abundance are therefore reflections of the ecological strategies of plants acting within the context of their biophysical environment. Since each species has a unique genetic make-up that codes for a species-specific set of traits and mechanisms, it is important to investigate the ecological strategies of individual species, particularly those that have significant impact on a vegetation community when abundant.

B. Abiotic environment

Climate is an important abiotic determinant of long-term trends in distribution and abundance of plant species. Climatic conditions (e.g. average temperatures, relative humidity and rainfall) vary both temporally and spatially across landscapes. Different plant species vary in their sensitivity to climatic factors due to differences in their physiological tolerances and ecological traits (Parmesan and Yohe 2003; Parmesan 2006); consequently, the suitability of different areas in the landscape for plant growth varies as a function of both the location-specific climatic conditions and the individual species tolerance for those conditions.

The availability of resources (e.g. water, light) is another important abiotic factor for plant growth (Daubenmire 1947; Gates 1980) that can affect the distribution and abundance of plant species. The availability of resources can fluctuate over space and time, and the extent of fluctuation can vary. Generally, when resources are not limiting, species abundance can increase. Conversely, when resources become limiting, shifts in abundance are dependent on the intrinsic traits of a species or its ecological strategies allowing it to maximize acquisition of the limiting resources (Bloom *et al.* 1985; Chapin *et al.* 1987; Smith and Huston 1989). Plant responses to individual resource gradients are well studied but the responses due to interacting effects of two or more resources are less understood (Holmgren *et al.* 2012). The effects of resource availability to species distribution and abundance can become interactive because resources are simultaneously present in nature. Understanding how resources impact plant performance independently or interactively will help us predict how disturbances and climate change, both of which alter resource availability (Sher and Hyatt 1999; Nicotra *et al.* 2010), might impact species distribution and abundance.

Topographic and edaphic factors can also influence plant growth, distribution, and abundance as these factors affect resource availability, particularly water and nutrients. Some topographic factors, e.g. elevation and slope aspect, are significantly correlated with climatic factors, hence influence from elevation and slope aspect are most likely an artefact of that high correlation. However, other topographic factors (e.g., slope gradient, ruggedness) are not significantly correlated with climate and could significantly affect edaphic conditions. For example, soil is prone to erosion in steep areas resulting in thinner soil devoid of organic-rich topsoil. Further, where slope is steep, soil moisture is likely to be low as water will drain down the slope. Soil functions as a reservoir of water and nutrients, and as anchorage for plants. Consequently, only those plants that can tolerate dry and nutrient-poor conditions and are able to anchor in thin soil would be able to colonize very steep habitats. Where the landscape is topo-edaphically heterogeneous, the growth, distribution, and abundance of species may vary significantly even over short distances (Cadiz and Buot 2011; Zhang *et al.* 2013; Horst *et al.* 2018; Nunes *et al.* 2019).

C. Biotic environment

Competition for resources is a biotic interaction that can lead to increases or decreases in the abundance of competitively superior or inferior species, respectively (Clements *et al.* 1929; Grace and Tilman 1990). Consequently, the competitively superior species can expand its niche, reducing the niche space available for the inferior one (Hutchinson 1957). Such dynamics were observed by Tilman (1987) in his experiment on the influence of nitrogen on the pattern of secondary succession in Cedar Creek, Minnesota, where the superior competitor *Agropyron repens* invaded and dominated high-nitrogen plots and displaced the dominant *Schizachyrium scoparium* and *Poa pratensis*. Similar pattern is reported for *Imperata cylindrica*. This grass is a highly competitive invasive species that directly competes with agricultural crops for major resources and impedes their growth through allelopathy (MacDonald 2004). Consequently, *I. cyclindrica* has become widely distributed and become dominant in many systems worldwide. Thus, shifts in species occupancy and abundance can happen when competition increases, and resources become limiting.

Herbivory is another important biotic factor that can limit plant growth, distribution, and abundance. At the individual level, the negative effects of herbivory on plant growth and reproduction is quite evident (Crawley 1989, 1997). At the population level, herbivory has been found to limit local plant abundance and distribution (Maron and Crone 2006). The extent of these herbivory effects are influenced by several factors, including the type of herbivores (Hulme 1994; Palmisano and Fox 1997; Bigger and Marvier 1998; Gomez and Zamora 2000; Sessions and Kelly 2001; Warner and Cushman 2002; Maron and Kauffman 2006; Maron and Crone 2006), plant life-history types (Mittelbach and Gross 1984; Reader 1993; Louda and Potvin 1995; Maron and Crone 2006), presence of environmental gradients (Lincoln and Mooney 1984; Galen 1990; Louda and Rodman 1996; Bruelheide and Scheidel 1999; Knight and Holt 2005; Maron and Crone 2006), and plant habitat types (Crawley 1997; Maron *et al.* 2002; Maron and Crone 2006). In other words, the effect of herbivory on plants can be highly context-dependent, hence the influence of herbivory on the growth, distribution and abundance of individual species may vary.

D. Disturbance

Disturbance can change the environmental conditions and resource availability in ecosystems, consequently altering habitat suitability, and therefore shifting the distribution and abundance of species. Disturbance refers to “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resource pools, substrate availability, or the physical environment" (White and Picket 1985). Disturbance varies in terms of frequency, intensity, size, timing (season of the year), and predictability, and the factors causing them are both endogenous and exogenous (Attiwill 1994). In a forest ecosystem, disturbance can range from a single tree-fall that creates a small canopy gap, to a severe fire that reduces canopy cover over a large area. Whichever the case, the disturbance elicits responses from the living components of the ecosystem, and these responses are either disturbance-specific (e.g. seed release in response to fire) (Gill 1981) or a general response to the changed environmental condition (e.g. regeneration of shade-intolerant species as light becomes available) (Yamamoto 2000), or a combination of both. Following a disturbance, shifts in distribution and abundance could occur. These shifts are more often determined by the initial floristic composition (Egler 1954; Noble and Slatyer 1977).

Small-scale disturbance, like a falling branch or whole tree, or the injury and death of trees, are common in forest ecosystems. Wind can also uproot and overthrow trees in what is known as a windthrow (Ulanova 2000). These create openings in the forest canopy, called gaps, which vary in size. Differences in gap size affect the pattern of plant growth in the gap mainly through the variation in the amount of light reaching the forest floor (Denslow 1980; Brokaw 1985; Canham *et al.* 1990; Abe *et al.* 1995). In general, the canopy gap creates a micro-environmental condition that favours the establishment of shade-intolerant species. Gaps could be exploited as well by opportunistic herbaceous understorey species that are widely distributed, albeit in low abundance, and could opportunistically become abundant with increased light and reduced competition. In a forest landscape, therefore, spatial heterogeneity occurring at small scales could also direct the distribution and relative abundances of plant species.

Fire is an important recurrent disturbance in some environments. For example, fire is a key ecological driver in the maintenance of the dry and wet eucalypt forests in Australia (Ashton 1976; Gill 1981). Many fire-adapted species get their cues for regeneration and germination from fire, and these fire-adaptive traits may only be present in a certain stage of their life cycle; hence, different fire regimes will have different effects on different species at different stages of their life cycle (Gill 1981). Since fire frequency, intensity, season, and type (Gill 1981; Gill and McCarthy 1998) interact with the intrinsic attributes of plant species, fire can primarily determine vegetation composition and abundance in fire-prone forests.

The effect of disturbance on plant distribution and abundance is not the same for all species but rather is dependent on their intrinsic attributes. Some species tend to favour disturbance, while others cannot tolerate them (Noble and Slatyer 1977). For example, invasive and weedy species tend to spread faster and increase in abundance with disturbance (Hobbs and Huenneke 1992; Sher and Hyatt 1999; Pivello *et al.* 2018). Conversely, the slow-growing pencil pine *Athrotaxis cupressoides* in Tasmania, Australia is extremely sensitive to fire and cannot survive high-intensity fire disturbances (Bliss *et al.* 2019; Bowman *et al.* 2019). This differential response highlights the importance of investigating disturbance impacts at the species level.

The role of climate change

Climate change is broadly defined as "any change in climate overtime whether due to natural variability or as a result of human activity" (Intergovernmental Panel on Climate Change or IPCC definition) (Pielke 2004). Globally, the predicted condition under continuous warming is such that the tropics become wetter while the sub-tropics and middle latitudes become drier (Putnam and Broecker 2017). Locally, in south-eastern Australia, a warming climate is predicted to decrease rainfall which would result in drier conditions (Suppiah *et al.* 2007; Whetton 2011). These changed conditions can alter habitat suitability, making it either less or more suitable for particular species depending on their tolerances to environmental conditions. Consequently, species may change their distribution and/or abundance. There is empirical evidence of shifts in the distributions of plants owing to recent climate change (Hughes 2000; Parmesan 2006; Bertrand *et al.* 2011; Chen *et al.* 2011; Doxford and Freckleton 2012; Gottfried *et al.* 2012; Zhu *et al.* 2012; Telwala *et al.* 2013; Settele *et al.* 2015; Lenoir and Svenning 2015; Kosanic *et al.* 2018). Species have shifted their distribution towards higher altitudes and higher latitudes, or eastward and westward, or unexpectedly towards lower altitudes (Parmesan 2006; Chen *et al.* 2011; Lenoir and Svenning 2015) as they track suitable habitats. Species either colonize new areas (at "leading edges") or become locally extinct (at "trailing edges") (Breshears *et al.* 2008; Settele *et al.* 2015; Lenoir and Svenning 2015). Empirical evidence also points to the impact of climate change on species abundance (Settele *et al.* 2015). For example, two native Antarctic plants *Deschampsia antarctica* (a grass), and *Colobanthus quitensis* (a cushion plant) have increased in abundance over recent decades (Smith 1994) due to increasing summer air temperatures (Fowbert and Lewis Smith 1994). In the Arctic tundra, shrub abundance has generally increased over broad areas due to warming (IPCC Working Group 2, Settele *et al.* 2015). On the other hand, decreases in abundance are predicted for populations at the "trailing" edges of a species range, where environmental conditions are becoming less suitable (Kelly and Goulden 2008; Breshears *et al.* 2008)

Climate change can also impact plant distribution and abundance indirectly through its effect on non-climatic factors such as disturbances (e.g. wildfire, drought, flood, cyclones) and biotic factors such as changes in the distribution of other species. Future climate scenarios are predicted to alter the frequency, severity and seasonality of disturbances such as wildfire, drought, flood, and cyclones (Allen *et al.* 2010; Bradstock *et al.* 2012; McColl-Gausden *et al.* 2021) and this could affect habitat suitability for particular species. Shifts in the distribution of other species caused by climate change, e.g. spread of invasive species (Hellmann *et al.* 2008; Settele *et al.* 2015), could also influence habitat suitability, e.g. by altering microclimate and soil properties (Weidenhamer and Callaway 2010; Gibbons *et al.* 2017). All these changes can alter species occupancy and abundance.

The direct and indirect effects of climate change on plant distribution and abundance depend on the tolerance of individual species to environmental changes. Hence, it is important to investigate these effects on individual plant species, more so on species whose dominance can greatly impact natural systems.

Research question, specific aims, and scope of the study

The broad aim of this thesis is to understand how a flammable native species can become prolific within its own range. This is achieved using a case study species – the native wiregrass – which is of high importance to forest flammability in south-eastern

Australia and grows prolifically under certain conditions. A conceptual model (Figure 1.2) about the drivers of wiregrass distribution and abundance is tested throughout the thesis using a mix of research methods. The conceptual model illustrates the relationships of the abiotic factors, disturbances, and biotic factors to distribution and abundance of wiregrass. These relationships are based on the results and inferences of past studies reported in the scientific literature.

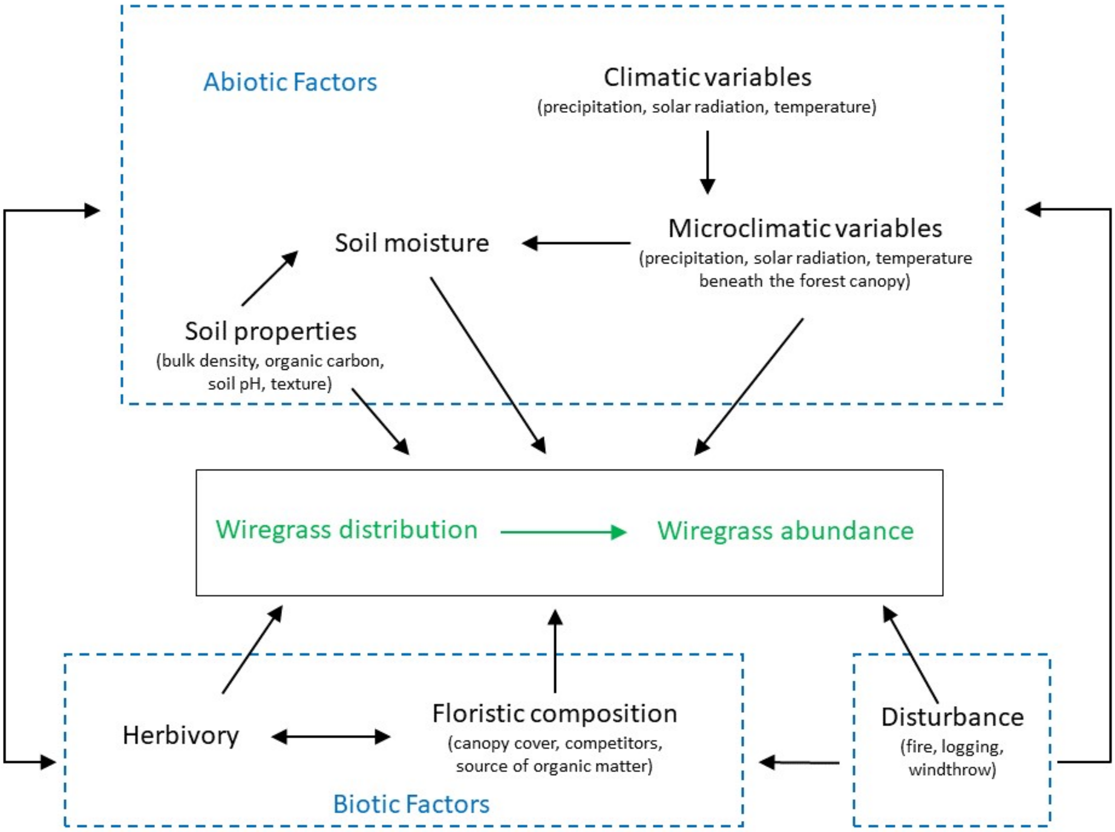


Figure 1.2 Conceptual model of the distribution and abundance of wiregrass *Tetrarrhena juncea* R. Br. as influenced by abiotic and biotic environmental factors and disturbance. The relationships depicted in this model are based on the results and inferences of past studies reported in the scientific literature. They will be tested and quantified throughout this thesis.

The overarching question addressed by this thesis is: *How does wiregrass become prolific within its own range?* This question is important to understand because wiregrass abundance has a positive influence on forest flammability (Buckley 1993; Fogarty 1993). Understanding under what conditions wiregrass can become abundant would potentially help fire managers to predict the likelihood of ignition, ease of suppression and spread of bushfire in forest communities with wiregrass.

Specifically, this study aims to investigate:

1. how environmental factors affect the distribution of wiregrass within its range;
2. how environmental factors influence the abundance of wiregrass within its range;
3. the effect of resource availability on wiregrass biomass; and,
4. the potential effect of climate change on wiregrass distribution and abundance.

The results are used to consider the implications for landscape flammability. This study focuses primarily on abiotic factors, disturbance and canopy cover, because there are many uncertainties regarding their influences on wiregrass distribution and abundance. This study does not incorporate the effects of other biotic factors, particularly vegetation composition and herbivory, because these have already been the focus of past studies (Atyeo 1972; Ashwell 1981, 1985; Ashton and Chappill 1989). This study also does not investigate the ecological strategies of wiregrass in relation to its growth, distribution, and abundance; nor investigate the importance of wiregrass abundance in forest flammability. The sheer volume of workload and the time needed to do all these things go beyond what can be handled in a time-constrained research project. The investigation on wiregrass abundance focuses on the wet forest (Mountain Ash-dominated forest) (Department of Environment Land Water and Planning 2021), where wiregrass is commonly present but at vastly different levels of abundance.

THE STUDY SPECIES – FOREST WIREGRASS *Tetrarrhena juncea* R.Br.

General description

Wiregrass is a native rhizomatous grass in south-eastern Australia that flowers during the warmer part of the year - between November and April (Walsh and Entwisle 1994). Wiregrass assumes different structural forms when abundant such as thick swards and stook-like structures climbing up to 6 m high over rigid supports e.g. tree trunks, tree ferns, tree stumps, and shrubs (Figure 1.3).

Motivations for studying wiregrass

Wiregrass is the focal study species for this research for three main reasons – (1) its positive influence on forest flammability, (2) its propensity for prolific growth, and (3) its broad distribution.

Wiregrass is considered by fire managers a critical fuel component because when abundant it contributes greatly to forest flammability (Sneeuwjagt and Peet 1985; Buckley 1993; Fogarty 1993). Abundant wiregrass influences flammability in the forests by increasing the fuel load and the continuity of the fuel bed, both horizontally (swards of wiregrass) and vertically (stook-like wiregrass). In addition, fires are more likely to ignite and spread at high surface fuel moisture contents when wiregrass is abundant (Buckley 1993). Most probably this is because wiregrass can have an aerated and elevated structure with a high fraction of suspended dead materials (Fogarty 1993). These suspended materials potentially have lower moisture content because they are more exposed to atmospheric drying than the fuel on the forest floor. Consequently, fires in wiregrass-dominated forests are sustained even with surface fuel moisture contents of greater than 20% (Buckley 1993) when fires would not usually propagate (Cheney and Sullivan 2008). This flammable characteristic of wiregrass coupled with the reported increase of wiregrass abundance after a fire disturbance (Stuwe and Mueck 1990) may create a positive flammability feedback loop, where fire promotes the abundance of a flammable species, which may in turn facilitates more fires (D'Antonio and Vitousek 1992; Rossiter et al. 2003). Owing to the high fire hazard posed by wiregrass, burn prescriptions specific to wiregrass-dominated forests have been developed (Buckley 1993) and are used by fire managers in current fire management. A greater understanding of the factors driving the distribution and abundance of wiregrass would assist fire managers in predicting likelihood of ignition, ease of suppression and spread of bushfire, yet this information is lacking.

Prolific growth of native wiregrass not only poses a risk to forest flammability but also to species diversity. High abundance of wiregrass in eucalypt forests is associated with low plant species diversity as dense swards prevent the establishment of other understorey species (Ashwell 1985; Bauhus *et al.* 2001). This includes species that are endangered and struggle to grow when wiregrass is dominant, e.g. *Pomaderris vacciniifolia* (Patykowski *et al.* 2014; Department of the Environment 2016).

The broad distribution of native wiregrass across south-eastern Australia (Figure 1.4) is another significant reason this is a critical research gap. If wiregrass were to become more prolific in these areas, then it has the potential to influence flammability across a heavily-populated and already highly flammable region of Australia. Wiregrass is typically present in low abundance but becomes opportunistically dominant for reasons that are poorly understood. Climate change and altered fire regimes could be the catalyst for this change in abundance. With a changing climate and altered fire regimes across the region, the broad occupancy of wiregrass could translate into higher abundance in the future, potentially altering the flammability of many different ecosystems.

Figure 1.3 Wiregrass in the understorey of the Mountain Ash-dominated forests in the Central Highlands of Victoria, Australia. a) Thick wiregrass sward interspersed with other species. b) Close-up of wiregrass sward. c) Wiregrass totally covering small plants and forming a mound (white arrow). d-e) “Stook” is the term for wiregrass climbing up over rigid supports.

Figure 1.4 Map of the distribution of wiregrass *Tetrarrhena juncea* R. Br. in Australian states per record of the Atlas of Living Australia ('Atlas of Living Australia' 2016).

Wiregrass dynamics and correlated factors

The factors controlling *wiregrass distribution* or occupancy are poorly understood and there are no studies which consider the factors driving occupancy across its full range. Wiregrass occupies both dry and moist habitats (Ashton 2000; Penman *et al.* 2009), shaded and open areas (Ashwell 1985; Buckley 1993; Ashton 2000) and occurs from sea level to the sub-alps (Willis 1970) in places with different aspects and slopes (Ashwell 1985; Ough and Ross 1992). Given this apparently broad ecological niche of wiregrass, its suitable habitats over south-eastern Australia may be widespread.

Although past studies identify several abiotic factors that influence *wiregrass abundance*, the relative importance of these factors is unclear (Figure 1.2). Ashwell (1985) showed that there was a relationship between the abundance of wiregrass and forest structure. However, the study was not able to resolve if soil moisture or amount of light is the more important driver of abundance. Furthermore, the influence of fire and other disturbances on wiregrass abundance is unclear. Some report an increase in wiregrass abundance following fire and other disturbance (Stuwe and Mueck 1990), while others report decreases in abundance after fire (Tolhurst 2003), and increases in the absence of fire (Penman *et al.* 2009). These seemingly contradictory results could be resolved by considering factors such as time since disturbance and the amount of available light at the forest floor. Increased availability of light after canopy disturbance is assumed responsible for stimulating thick growth of wiregrass (Lamp *et al.* 2001). Clearly, the role that environmental factors play on the tendency of wiregrass to become highly abundant in certain areas where it occupies is not well-understood. This poor understanding should be addressed because of the flammability risk this species poses when abundant.

THESIS STRUCTURE

This study consists of an introduction, three data chapters, and a general discussion chapter. Figure 1.5 illustrates how the three data chapters are linked to address the overarching research question.

In Chapter 2, I investigate the key factors influencing the current distribution of wiregrass in its current geographical range using MaxEnt modelling of present-background data. Based on this MaxEnt model, I identify the factors and conditions associated with the suitable habitat of wiregrass. I also predict how wiregrass is distributed under current and future climate conditions.

In Chapter 3, I investigate the key environmental factors influencing wiregrass abundance. I develop a generalized additive model (GAM) of wiregrass cover surveyed in Mountain Ash-dominated forest, which is a forest type where wiregrass is commonly present but varies greatly in abundance. Based on the results, I discuss the conditions under which wiregrass becomes abundant and the potential of wiregrass to initiate a positive flammability feedback loop.

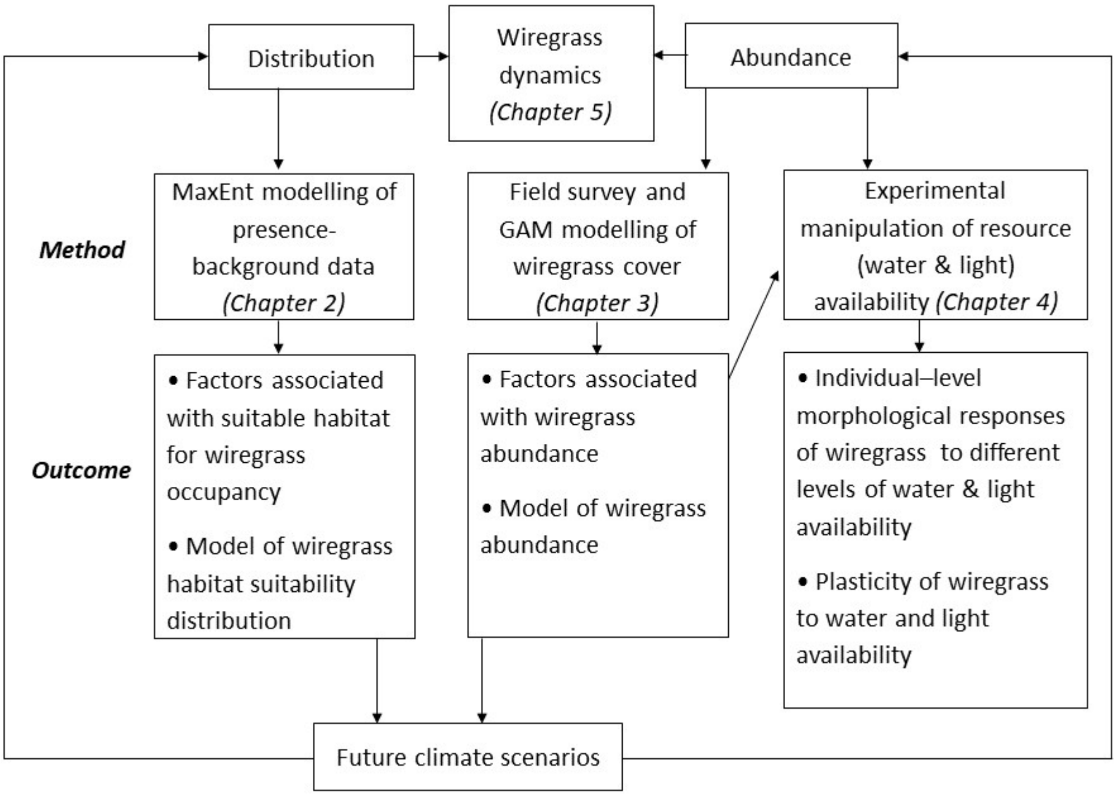


Figure 1.5 Overview of the thesis structure including the methodological approach and expected outcomes of the three data chapters.

In Chapter 4, I investigate in detail the two factors (water and light) whose availability in the understorey is affected by canopy cover (which was the second factor influencing wiregrass abundance identified in Chapter 3) and could change under future climate conditions and an altered disturbance regime. The effects of water and light on wiregrass growth, survival, biomass allocation and leaf morphology were investigated through experimental manipulation. The results give an understanding on how wiregrass abundance, via growth and survival, may respond to changing light and moisture levels, and the implications of conditions under future climate and forest disturbance on wiregrass abundance.

In Chapter 5, I develop a conceptual understanding of the dynamics of wiregrass distribution and abundance as affected by correlated factors under current conditions based on the insights gained from the results in Chapters 2 to 4. I then discuss how wiregrass can become prolific within its range and use this insight to contribute to the broad discussion on how native species can be released from environmental constraints of abundance to become potentially weedy. I also predict the possible trajectory of effects of future climate scenarios on the distribution and abundance of wiregrass and their implications to forest flammability. Lastly, the limitations of this thesis and future research directions are discussed.

2 Environmental factors associated with the distribution of forest wiregrass *Tetrarrhena juncea* R.Br.

Unpublished. Prepared in paper format for submission to a peer-reviewed journal.

ABSTRACT

Forest wildfire is, in part, a function of the flammability of species and the structure of the vegetation community. Understanding the factors that drive the distribution of flammable species is important for predicting forest flammability and consequent wildfire risk. This study employed a correlative species distribution modelling using MaxEnt algorithm to investigate the environmental factors that affect the distribution of the native forest wiregrass *Tetrarrhena juncea* R.Br., (hereafter *wiregrass*), a key species of concern for flammability in south-eastern Australia. The model was also used to predict wiregrass distribution under future climate scenarios. Five climatic factors (temperature seasonality, precipitation of the driest month, rainfall seasonality, annual mean temperature, and minimum temperature of the coldest month) and soil pH were identified as significant factors associated with the distribution of wiregrass. Under future climate, wiregrass distribution is predicted to contract southward of its current range. Range shift and associated local extinctions are two of the possible impacts of climate change on wiregrass distribution. Where there are associated changes in abundance with the altered future distribution of wiregrass, it may also influence community scale flammability.

INTRODUCTION

Wildfire is a key disturbance in forests, influencing the diversity, structure, and function of vegetation communities (Bond and Keeley 2005). The ignition, spread, and intensity of a wildfire depends, in part, on the flammability of the vegetation community, and this is dependent on the composition and structure of the vegetation (fuel) (Pausas *et al.* 2017). Plant species differ in their flammability owing to traits including foliage moisture content, volatile oils, leaf size, and plant architecture. When two or more species occur together, the combined effect of their traits on flammability can be non-additive as some species disproportionately affect the flammability of a species mix; this has been demonstrated at laboratory and field-scales (Schwilk and Caprio 2011; Pérez-Harguindeguy *et al.* 2013; Wyse *et al.* 2017). Within a vegetation community, the influence of a plant species on vegetation structure is important to flammability (Gill and Zylstra 2005; Zylstra 2011). Fire is likely to spread faster horizontally when there is continuous cover of live and dead vegetation rather than when cover is patchy (Keane 2015). Similarly, fire is likely to spread faster vertically when there is continuous vegetation linking the litter bed to the tree crown (referred to as ladder fuels) (Husari *et al.* 2006) rather than when the mid-storey is open. Many invasive grasses increase the continuity of vegetation cover resulting in increased fire rates of spread, frequency and extent' (Brooks *et al.* 2004). Understanding the factors that drive the distribution and abundance of these species is important for predicting forest flammability and consequent wildfire risk.

The distribution of any plant species is a function of its ecological niche, which is a set of ecological requirements that the species need to survive and reproduce (Grinnell 1917; Hutchinson 1957; Vandermeer 1972; Brown 1984; Hall *et al.* 1992; Hirzel and Le Lay 2008). For plants, these requirements include light, soil, and climatic factors (temperature, precipitation/moisture) (Lambers *et al.* 2008). Light is crucial for plant productivity, while soil contains the nutrients needed for plant growth (Lambers *et al.* 2008). Climate has long been recognized as an important driver of species distributions at regional and continental scales (Pearson and Dawson 2003). Consequently, climate change is predicted to significantly impact species distribution (Hughes 2000; Parmesan 2006; Chen *et al.* 2011; Lenoir and Svenning 2015; Kosanic *et al.* 2018). Climatic factors are particularly important for plants because plants are immobile and cannot move to avoid adverse conditions.

Correlative species distribution modelling (SDM) allows for the identification of the significant factors associated with the distribution of species (Peterson 2006). Although correlative modelling does not have the ability to identify the real causal factor, we can infer from correlative SDMs the basic ecological requirements of species (Peterson 2006; Elith and Leathwick 2009; Guillera-Arroita *et al.* 2015). The selection of predictors that are ecologically relevant to the species is critical for deriving good inferences from SDMs (Elith and Leathwick 2009). SDM enables predictions of current and potential future distribution of species. These outputs can be used to identify highly suitable areas that satisfy the best ecological conditions for a species to survive and reproduce (Hirzel and Le Lay 2008). A 'highly suitable habitat' is more likely to hold high abundance of the species (Whittaker 1975; Hengeveld and Haeck 1982; Weber *et al.* 2017), particularly when significant site-specific factors influencing abundance are present (Duff *et al.* 2011; Tanner *et al.* 2017; Cadiz *et al.* 2020). In that case, areas identified as 'highly suitable habitats' of flammable species may become potential sites of increased flammability. As such, an SDM for these species could be used to target fuel monitoring and management programs and prepare for future risks with changing climate.

Wiregrass is a key species of concern for flammability in south-eastern Australia (Buckley 1993; Fogarty 1993). It is a highly flammable understorey native grass that can greatly increase the horizontal and vertical continuity of live and dead vegetation in a forest when abundant. It can form thick swards on the forest floor and can engulf shrubs and herbaceous species (Ashwell 1981). It can also grow up and over rigid supports like tree ferns, shrubs, and tree trunks (Ashwell 1981) up to 6 meters high. It occurs across the south-eastern portion of Australia in forested areas that experience recurrent fires ('Atlas of Living Australia' 2018).

This study aims to investigate the environmental factors that affect the distribution of wiregrass within its natural range by using correlative SDM. Specifically, this study 1) identifies the key factors associated with the distribution of wiregrass; and 2) predicts the distribution of wiregrass for current and future climatic conditions.

METHODS

Study species

Wiregrass has a wide geographic range in south-eastern Australia. It is a common native species in the ground stratum of wet forests (Petrie *et al.* 1929; Cunningham and Cremer 1965; Ashton 1976; Feller 1978, 1980; Adams and Attiwill 1984; Ashwell 1985; Ough and Ross 1992; Ough and Murphy 1996; McKenzie and Kershaw 1997; Serong and Lill 2008), dry sclerophyll forests (Gill and Ashton 1971; Feller 1978; Neumann and Tolhurst 1991; Penman *et al.* 2008, 2009), heaths and scrubs (Ashton and Webb 1977), foothill and coastal forests (Buckley 1993; Fogarty 1993), *Eucalyptus obliqua* forests (Petrie *et al.* 1929; Attiwill *et al.* 1978; Bi and Turvey 1994), and pine plantations (Barnett 1978). It is a perennial understory grass that is capable of both vegetative and sexual reproduction. It flowers during the warmer part of the year (between November and April) (Walsh and Entwisle 1994). It occurs in both dry (Penman *et al.* 2009) and moist habitats (Ashwell 1985; Ashton 2000), in both shaded and open areas from sea-level to the sub-alpine regions (Willis 1970) in areas with varying slope, aspect and irradiance (Ashwell 1985; Ough and Ross 1992).

Study area

This study encompassed the entire geographic range of wiregrass in south-eastern Australia as reported in the Atlas of Living Australia (‘Atlas of Living Australia’ 2018). Climate across the study area ranges from temperate (Victoria, South Australia, Australian Capital Territory, New South Wales, and Tasmania) to more tropical (Queensland). The study area is associated with *Eucalyptus* forests where periodic fire is part of the ecosystem processes. Fires in this region occur less frequently (intervals > 20 years) than in northern Australia (intervals < 5 years), but at very high intensities, typically between 5,000 to 10,000 kW m-1 or extremely at more than 50,000 kW m-1 crown fires (Russell-Smith *et al.* 2007; Bradstock 2010; Bradstock *et al.* 2012; Murphy *et al.* 2013; Fairman *et al.* 2016). Fires typically occur in the summer months (December – February) (Murphy et al. 2013). Large, damaging bushfires within this region have occurred throughout recorded history (Collins 2009; Blanchi *et al.* 2014). However, evidence suggests the interval between these fires has become smaller since the early 2000s (Fairman *et al.* 2016; Sharples *et al.* 2016; Lindenmayer and Taylor 2020; Abram *et al.* 2021; Canadell *et al.* 2021; Richardson *et al.* 2021). The large-scale fires include the most recent Black Summer (2019/2020) fires where 7.2 million hectares were burnt across south-eastern Australia (Nolan *et al.* 2021), equating to at least 21% of Australia's temperate forests (Boer *et al.* 2020).

Data for modelling

Presence records for wiregrass were used to model the distribution of wiregrass. Data were obtained from the Atlas of Living Australia ('Atlas of Living Australia' 2018), which included 15,137 records of wiregrass occurrences. Records were removed where they had poor accuracy (> 250 m coordinate uncertainty) or occurred in cleared or non-native vegetation based on NVIS 4.1 Major Vegetation Groups (Department of the Environment 2012). A further 11 records in South Australia were excluded because wiregrass is likely to be introduced in this region (Jessop *et al.* 2006). The remaining records were then randomly thinned so that locations were separated by a minimum distance of 5 km to minimize spatial dependence and survey bias. This produced a final data set of 986 presence records across the species' range.

A set of environmental spatial data layers consisting of temperature, moisture, edaphic, and light variables (resolution of 9 arc-sec, approximately 281 m) were selected as potential predictors of habitat for wiregrass (Table 2.1). Plants directly or indirectly respond to these four factors physiologically (Lambers *et al.* 2008). For temperature and moisture, the potential predictors were those relating to annual total inputs (annual mean temperature, annual precipitation), those that describe variability patterns that may cause stress to wiregrass (temperature seasonality, annual mean diurnal range, precipitation seasonality), and those that describe extreme events that may limit wiregrass distribution (maximum temperature of warmest month, minimum temperature of coldest month, precipitation of driest month). The edaphic factors chosen were indicators of nutrient availability (organic carbon, clay, soil pH) and water availability (available water capacity, bulk density, clay) to plants. Topographic variables were also included to check if they exert any influence on the distribution of wiregrass, which occurs from sea-level to the sub-alps (Willis 1970) in places with different aspects and slopes (Ashwell 1985; Ough and Ross 1992). Highly correlated variables (> 0.7) were identified (Appendix 1), and the less important variable in terms of ecological reasoning was removed (Green 1979; Dormann *et al.* 2013). This was done by selecting the proximal over the distal variable (Austin 2002, 2007). Austin (2002) defines proximal and distal as “the position of the predictor in the chain of processes that link the predictor to its impact on the plant” – proximal being the more causal variable determining plant response than the distal. Variables in **bold** in Table 2.1 were the final set of predictor variables after removing correlated variables.

Table 2.1 Potential predictors for the species distribution modelling (SDM) process. Variables included in building the model after exclusion of highly correlated variables are in **bold**.

Variables	Definitions	Units	Source
Temperature			
Annual mean diurnal range	Mean of the weekly diurnal temperature ranges	degrees Celsius	Bioclim v 6.0
Annual mean temperature	Mean of weekly temperature	degrees Celsius	Bioclim v 6.0
Maximum temperature of warmest period	Highest maximum temperature in all weeks of the year	degrees Celsius	Bioclim v 6.0
Minimum temperature of coldest period	Lowest minimum temperature of the year	degrees Celsius	Bioclim v 6.0
Temperature seasonality	Standard deviation (SD) of the weekly temperature	degrees Celsius	Bioclim v 6.0
Moisture			
Annual mean moisture index	Mean of weekly moisture index values 0-1	none	Bioclim v 6.0
Annual precipitation	Mean annual precipitation	millimetres/ year	Bioclim v 6.0

Variables	Definitions	Units	Source
Mean moisture index of driest quarter	Average moisture index (0-1) of the quarter with the lowest moisture index	none	Bioclim v 6.0
Mean moisture index of wettest quarter	Average moisture index (0-1) of the quarter with the highest moisture index	none	Bioclim v 6.0
Precipitation of driest period	Precipitation of the driest month	millimetres	Bioclim v 6.0
Rainfall seasonality	Standard deviation (SD) of the weekly rainfall	millimetres	Bioclim v 6.0
Summer rainfall	Precipitation falling in summer months	millimetres	Bioclim v 6.0
Winter rainfall	Precipitation falling in winter months	millimetres	Bioclim v 6.0
Edaphic			
Available water capacity	Maximum amount of water stored in a soil profile that can be used by plants	%	CSIRO (Viscarra Rossel *et al.* 2015)
Bulk density – whole earth	Bulk density of the whole soil (including coarse fragments) in mass per unit volume by a method equivalent to the core method	g cm^{-3}	CSIRO (Viscarra Rossel *et al.* 2015)
Clay	< 2 um mass fraction of the < 2 mm soil material using the pipette method	%	Keith 2011
Organic carbon	Mass fraction of carbon by weight in the < 2 mm soil material as determined by dry combustion at 900 Celsius	%	CSIRO (Viscarra Rossel *et al.* 2015)
Soil pH ($CaCl_2$)	pH of a 1:5 soil/0.01M calcium chloride extract	none	CSIRO (Viscarra

Variables	Definitions	Units	Source
			Rossel *et al.* 2015)
Light			
Highest weekly radiation	Largest weekly solar radiation estimate	W / m^2	Bioclim v 6.0
Topographic			
Elevation	Height above sea level	m	Keith 2011
Ruggedness	Standard deviation of the elevation	none	Keith 2011
Slope	Slope of the ground	degrees	Keith 2011

Modelling the current distribution of wiregrass

Correlative SDM was performed to identify the most important abiotic variables associated with the distribution of wiregrass and predict its distribution. This was undertaken using the Maximum Entropy (MaxEnt) algorithm (Phillips *et al.* 2006). MaxEnt was chosen as it has high predictive powers based on presence-only data (Elith *et al.* 2006).

A set of background points were sampled to characterize the environment in our study region (Phillips *et al.* 2006; Elith *et al.* 2011). A set of 22,799 background points were sampled from within the Interim Biogeographical Regionalisation for Australia (IBRA) bioregions where the presence records fell. Only those points in extant vegetation were included. Any background points located more than 0.5 degree of latitude above the northern most wiregrass record were excluded.

SDMs with different subsets of predictors (in **bold** in Table 2.1) were then fitted using the MaxEnt algorithm (Phillips *et al.* 2006). Hinge features were used to build models with smoothed responses that extrapolate in a biologically realistic manner (Elith *et al.* 2010; Swan *et al.* 2021). Variables with small contributions (< 5 %) were removed, further reducing the number of final predictor variables from eleven to six, and the models were re-fitted. Model fit was evaluated using the area under the receiveroperating characteristic curve (AUC), where values between 0.8 and 0.9 signify models with a good fit and those over 0.9 with an excellent fit (Thuiller *et al.* 2003).

Predicting the current and future distribution of wiregrass

The MaxEnt model output was used to predict the baseline distribution of wiregrass under current climatic conditions. Future distributions under high (A1F1) and mid-range (A2) greenhouse gas emission scenarios (IPCC 2000) were also predicted for the years 2030, 2050, 2070 and 2100 using the climate projections from four global circulation models (GCMs): CSIRO-Mk3, GDFL-CM2, MPMP-ECHAM5, and UKMOHADCM3. These GCMs are appropriate to use over the Australian region because they effectively simulate the observed average (1961-1990) patterns of mean sea-level pressure, temperature and rainfall in the region (Suppiah *et al.* 2007). The use of an ensemble of GCMs is a current approach used to address the uncertainty of predictions contributed by GCMs (Diniz-Filho *et al.* 2009; Forester *et al.* 2013; Porfirio *et al.* 2014; Thuiller *et al.* 2019)

The distribution output was used to determine the suitability of habitat for wiregrass. The predicted suitable habitat was categorized to determine spatial changes in areas that have high, moderate, and low suitability for wiregrass. A minimum threshold of habitat suitability for occupancy of 0.3 was established using the maximum training sensitivity plus specificity parameter (Liu et al., 2005). Habitat suitability was arbitrarily categorized into high suitability (≥ 0.6), moderate suitability (0.4 – 0.6), low suitability (0.3 – 0.4), and unsuitable (< 0.3). Changes in spatial extent of the different suitability categories under the different future climate scenarios were calculated as unweighted averages of predictions from the four GCMs.

All analyses were performed using R version 3.5.1 (R Core Team 2018).

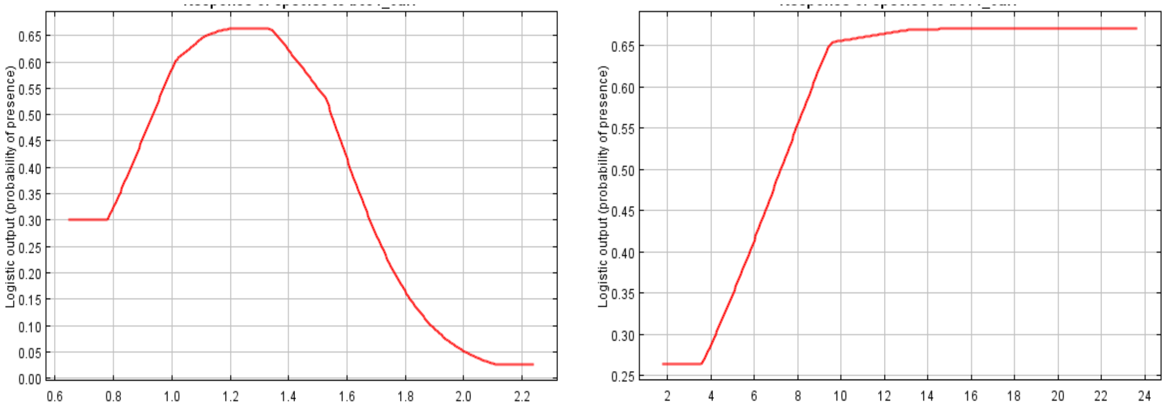
RESULTS

The MaxEnt final model of wiregrass distribution included six variables – five climatic variables and one soil variable (Table 2.2). The primary contributors to the model were temperature seasonality (40.4 % contribution), precipitation of driest month (20.3% contribution), rainfall seasonality (14.5% contribution), and annual mean temperature (10.7% contribution). The other two variables, soil pH and minimum temperature of the coldest month, had a combined contribution of 14.1%. The model had a good fit, hence, high discrimination capacity, with AUC = 0.86 both on training and test data.

Table 2.2 Estimates of relative contributions of the final set of predictors in the MaxEnt model predicting wiregrass distribution.

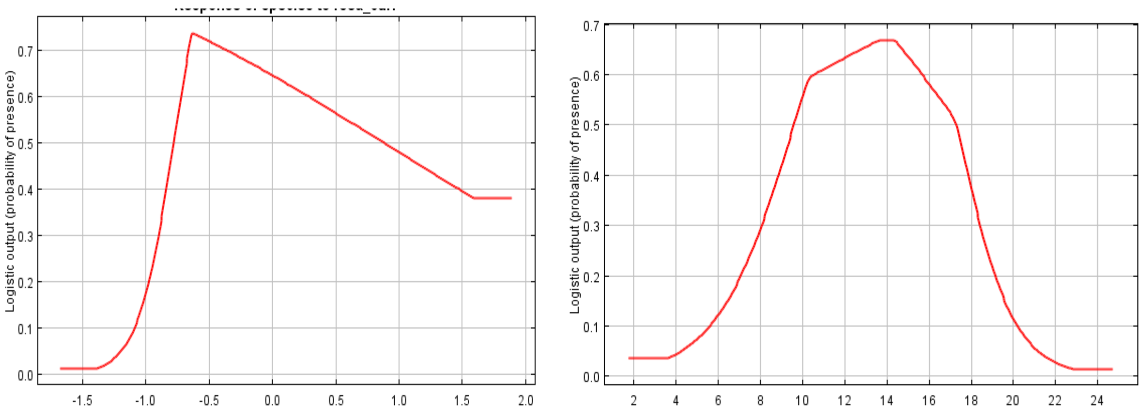
Variable	Percent contribution
Temperature seasonality	40.4
Precipitation of driest month	20.3
Rainfall seasonality	14.5
Annual mean temperature	10.7
Soil pH	8.7
Minimum temperature of coldest month	5.4

The responses of wiregrass to the predictor variables were non-linear (Figure 2.1). Wiregrass is most likely found in areas with less temperature variation (Figure 2.1a), with annual mean temperature within 8 to 18 °C (Figure 2.1d), and minimum temperature of coldest month not falling below -4 °C (Figure 2.1f); with rainfall seasonality approximately between -0.9 to 1.6 (Figure 2.1c) and the lowest precipitation of driest month not falling below 4 mm/month (Figure 2.1b); and with pH less than 5.3 (Figure 2.1e). Relative to the background environment, the suitable habitat for wiregrass has lower annual mean temperature (Appendix 2d), higher mean precipitation of the driest month (Appendix 2b), lesser mean rainfall variation (Appendix 2c), and lower soil pH (Appendix 2e).



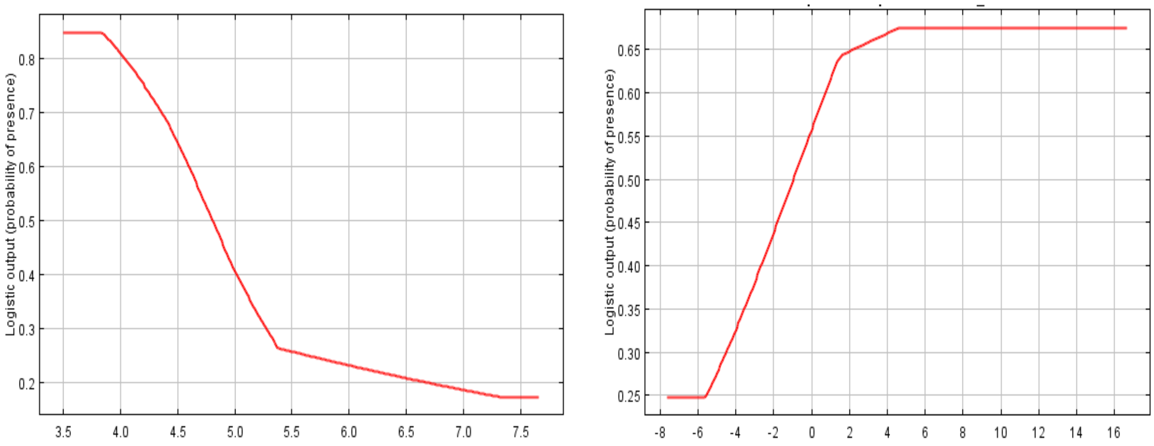
a. temperature seasonality

b. precipitation of driest month



c. rainfall seasonality

d. annual mean temperature



e. soil pH

f. minimum temperature of coldest month

Figure 2.1 Response curves to a) temperature seasonality, b) precipitation of driest month, c) rainfall seasonality, d) annual mean temperature, e) soil pH, and f) minimum temperature of coldest month. The curves show how the logistic prediction changes as each environmental variable is varied, keeping all other environmental variables at their average sample value.

Figure 2.2B shows the MaxEnt prediction of wiregrass distribution under current climatic conditions with the occurrence points of wiregrass in south-eastern Australia (Figure 2.2A). Victoria has the largest predicted area of highly suitable habitat for wiregrass. This is concentrated in the southern half of Victoria and includes major forested National Parks such as Great Otway National Park, Yarra Ranges National Park, Dandenong Ranges National Park, Bunyip State Park, Wilsons Promontory, and Croajingolong National Park. In New South Wales, areas in the south-east are predicted to be highly suitable for wiregrass. In Tasmania, highly suitable areas are found in the northeast, central west, and south. A small portion of highly suitable areas are found in south-eastern Queensland.

Eighty-nine percent (89%) of the known sites of wiregrass were predicted as suitable habitat (Figure 2.2). Of these suitable habitats, 57% were highly suitable, 35% were moderately suitable, and 8% had low suitability. Eleven percent (11%) of the known sites of wiregrass were predicted to be unsuitable habitat.

Under current climatic conditions, the predicted area of moderately suitable habitat was approximately half the total area of suitable habitats, low suitable habitat was approximately 30%, and highly suitable habitat was approximately 20% (Figure 2.3). These proportions relative to the total suitable habitat remained consistent under future climate scenarios but the future area relative to the current area was predicted to consistently decrease from 2030 to 2100 (Figure 2.3).

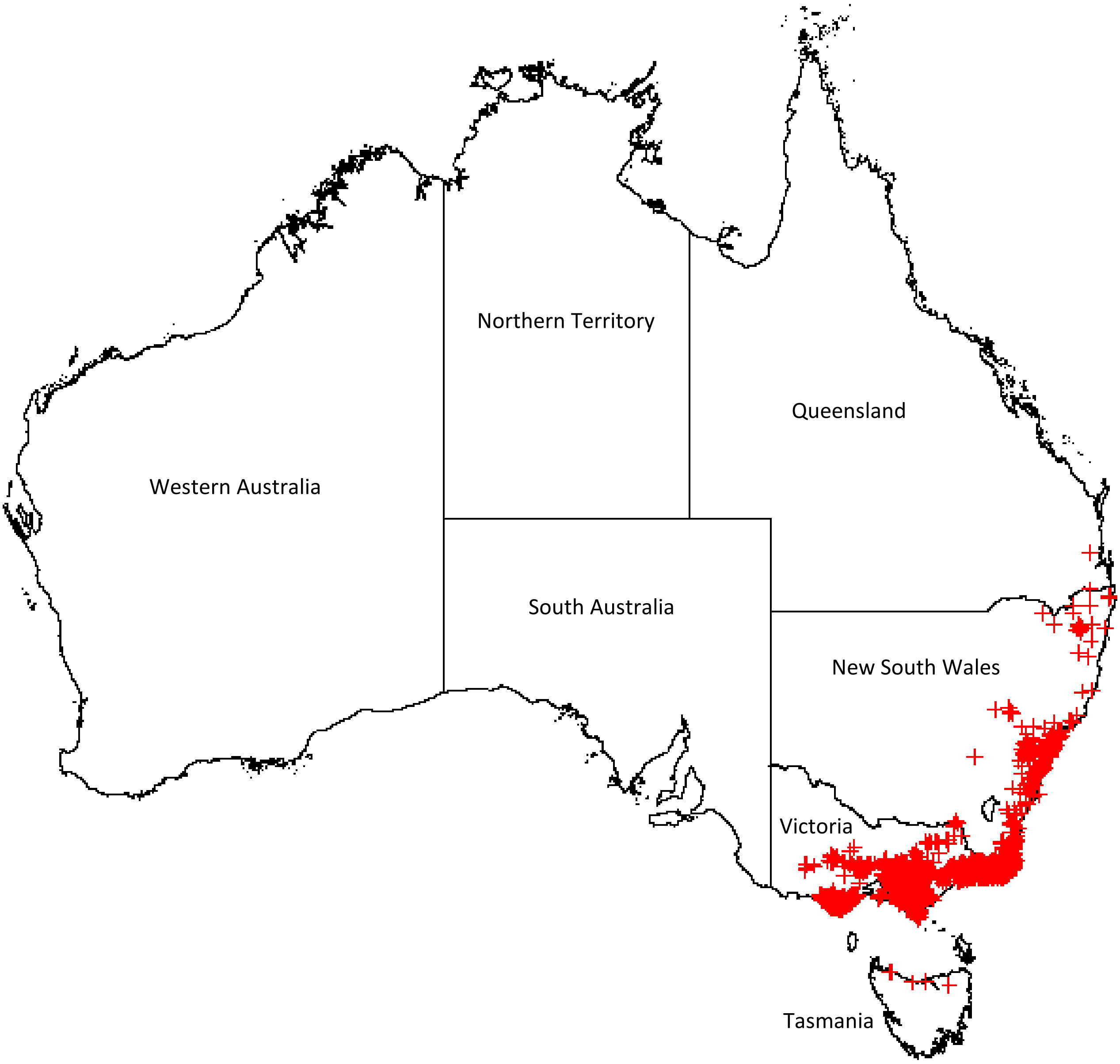


Figure 2.2 A) Distribution of forest wiregrass *Tetrarrhena juncea* R.Br. in Australia per record of the Atlas of Living Australia ('Atlas of Living Australia' 2018).

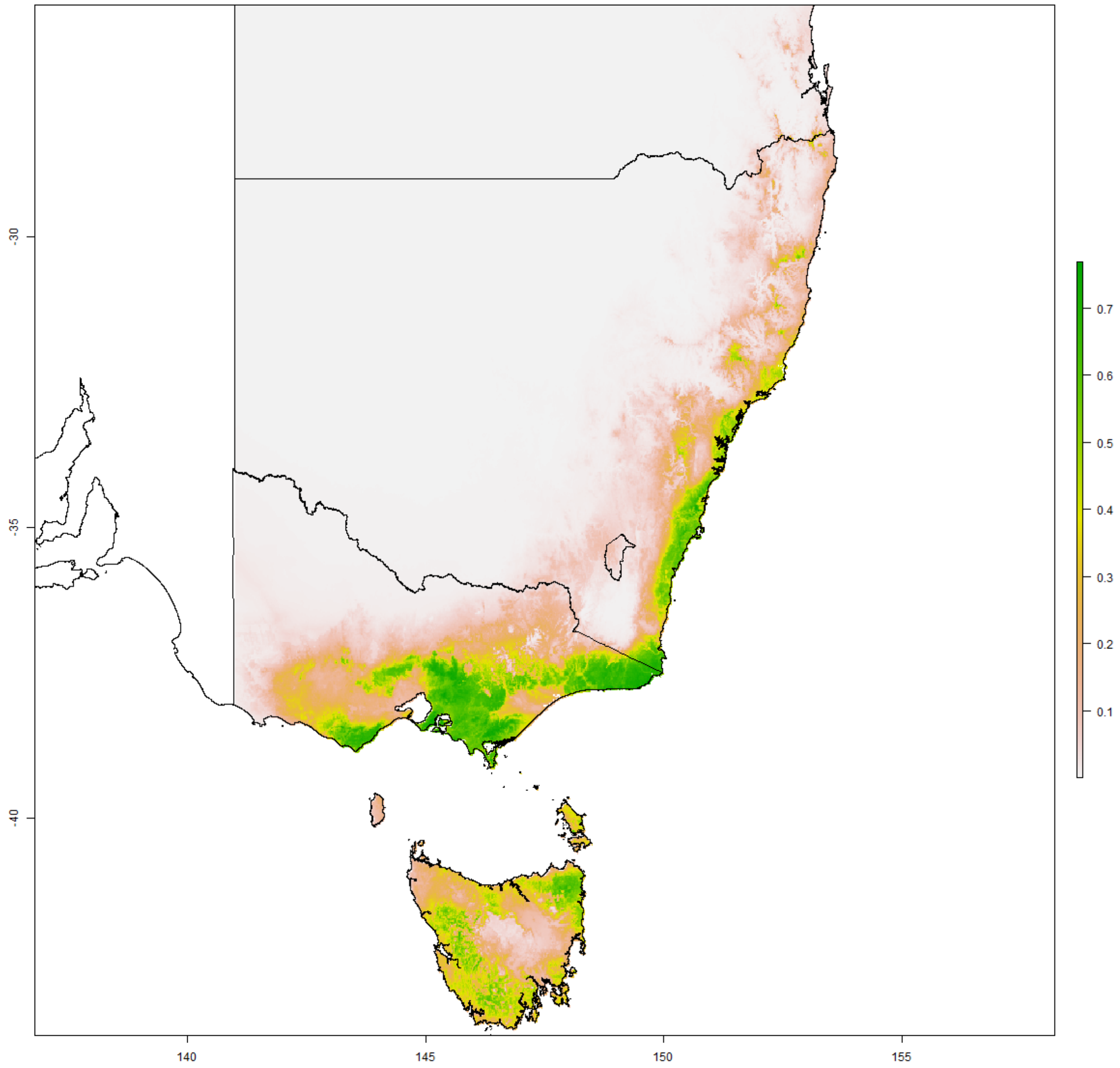


Figure 2.2 B) MaxEnt prediction of habitat suitability for *Tetrarrhena juncea* R.Br. under current climatic conditions in southeast Australia. The colour indicates the habitat suitability of the area to wiregrass – green being the highly suitable habitat. The state of Victoria has the largest predicted area of highly suitable habitat for wiregrass.

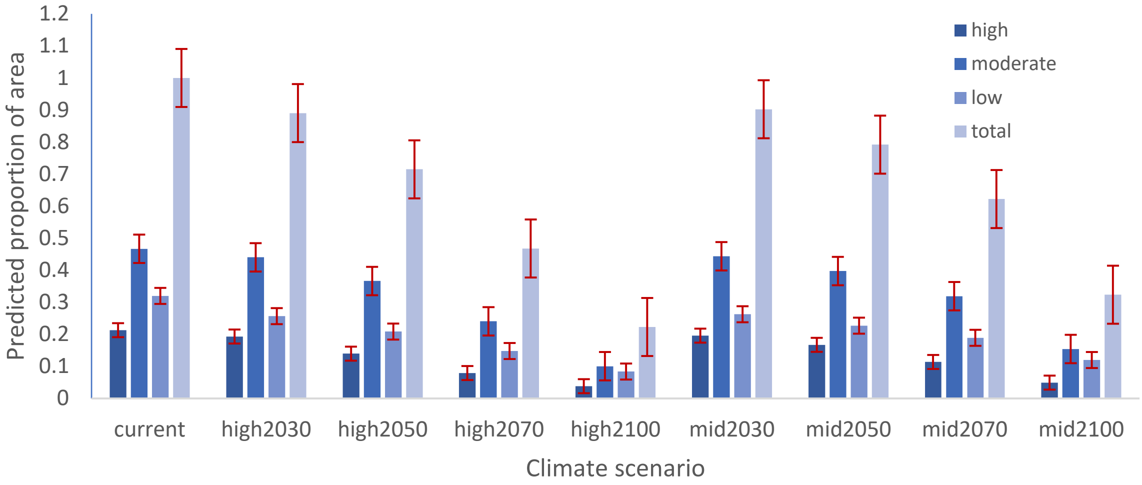


Figure 2.3 MaxEnt prediction of habitat suitability for wiregrass under current conditions and future climate scenarios of high and mid-range greenhouse gas emissions (A1F1 and A2, respectively; IPCC 2000) in years 2030, 2050, 2070, and 2100. Future predictions of percent area change relative to the current prediction are unweighted averages from the ensemble of predictions of four global circulation models (GCMs). The total suitable habitat is broken down into *high, moderate,* and *low suitability* per climate scenario per prediction year.

All predictions of future wiregrass distribution using the climate projections from the four GCMs consistently showed wiregrass distribution contracting southwards under both the high and mid-range greenhouse gas emission scenarios (Appendix 3). In this southern range, the prediction of distribution using climate projections from MPMP-ECHAM5 showed an expanding area of highly suitable habitat for wiregrass in southwestern Tasmania. Generally, the reduction of predicted total suitable habitat under future climate scenarios relative to the current prediction (Figure 2.2) was higher under the high greenhouse gas emission scenario by at least 1% (in 2030) and at most 15% (in 2070) than under mid-range scenario. Under the high greenhouse gas emission scenario, the percentage of reduction of total suitable habitat per prediction year relative to the current total area had an increasing trend from 11% in 2030, 18% in 2050, and 25% in both 2070 and 2100. The same trend was predicted under the mid-range greenhouse gas emission scenario, but the reduction was generally lower, from 8% in 2030, 11% in 2050, 18% in 2070, and 30% in 2100.

DISCUSSION

Climate is an important predictor of habitat suitability for wiregrass and is therefore a key determinant of its distribution. In the predicted current distribution, a large portion of highly suitable habitat for wiregrass is within Victoria. The area of highly suitable habitat is predicted to decrease and contract to the southern portion of the range under future climate scenarios, with a possible expansion of highly suitable habitat in southwestern Tasmania.

Key factors associated with suitable habitat for wiregrass

Temperature and moisture are significant climatic factors linked with suitable habitat for wiregrass. Three of the five climatic variables in the species distribution model were temperature-related: temperature seasonality, annual mean temperature, and minimum temperature of the coldest month. Temperature seasonality was the most important factor in the model, which showed that wiregrass is likely to thrive in habitats with less temperature variation. Moisture is another critical factor with two rainfall variables in the best model: precipitation of driest month and rainfall seasonality. Our results suggest that although wiregrass can persist under dry conditions, moister conditions are preferable. This result aligns with the results of field-based studies where wiregrass has been found to occur in both dry and wet eucalypt forests (Ashton 2000; Penman *et al.* 2009) but is reportedly more prolific in the wet forests (Atyeo 1972; Ashwell 1985).

The requirement for cool temperatures coupled with high moisture for areas of highly suitable habitat reflects that wiregrass is a C_3 grass. Hattersley (1983) investigated the distribution of C_3 and C_4 grasses in Australia in relation to climate and found that C_3 grasses pre-dominate in areas with a cool and wet spring such as in Victoria, Tasmania, and south-western slope of New South Wales. C_4 grasses, on the other hand, pre-dominate in areas with a hot and wet summer such as in the Northern Territory and Queensland. Unlike C_4 plants, C_3 plants cannot efficiently photosynthesize at high temperatures and very low moistures because they do not have the mechanism to counter the negative effect of these conditions to photosynthesis (Taiz and Zeiger 2002). Hence, C_3 grasses are best adapted to relatively cool and wet environments.

Soil pH is the only edaphic factor associated with the distribution of wiregrass. Soil pH of the whole study area ranges from neutral to very acidic, but the suitable habitat of wiregrass is associated with very acidic soil (pH < 5.5). Generally, plants prefer slightly acidic soil because nutrients become bio-available to them at the pH range of 5.5 to 6.5 (Taiz and Zeiger 2002). Toxic quantities of aluminium and manganese are present in very acidic soils and are harmful to most plants (Taiz and Zeiger 2002; Lambers *et al.* 2008). Consequently, soil pH has long been recognised to affect the distribution of plants and plant assemblages (Kurz 1930; Hageer *et al.* 2017; Buri *et al.* 2017) because of its role in nutrient bio-availability, metal mobility, toxicity, and plant growth (Lambers *et al.* 2008). Soil pH was also identified as a key predictor of fuel properties across south-eastern Australia (McColl-Gausden *et al.* 2020). Studies show that the inclusion of soil predictors in SDMs for a range of plant species significantly improves the predictive performance of the models (Hageer *et al.* 2017; Buri *et al.* 2017), suggesting that soil variables exert significant influence over species distributions, hence defining habitat suitability. That said, soil variables are often derived from climate and topographic predictors (Viscarra Rossel *et al.* 2015) and therefore their importance in the model could merely reflect the effect of these other factors rather than the soil properties *per se*. Hence, wiregrass may either be an acidophile, or maybe its ‘preference’ to very acidic soil, as indicated in the model, is just a reflection of its preference to the climatic and topographic factors used to derived the soil pH measurement.

Wiregrass distribution under current conditions

The high concentration of highly suitable areas in the state of Victoria is likely to be partially an artefact of sampling bias since a large portion of the distribution data are found here. Nonetheless, these areas of highly suitable habitat indicate locations where wiregrass is more likely to be abundant and more likely to influence the flammability of forest ecosystems. Further research is required to better understand wiregrass dynamics in these highly suitable habitats as site-specific factors are likely to control wiregrass abundance (Duff *et al.* 2011; Tanner *et al.* 2017; Cadiz *et al.* 2020). This is the topic of Chapter 3, where wiregrass abundance was assessed in highly suitable habitats in Victoria. Such assessment of abundance is also highly recommended in forested areas which are highly suitable, e.g., in northeast, central west, and south of Tasmania.

The distribution of wiregrass in areas that were predicted as unsuitable could be an artefact of data limitations in the modelling process. First, the data used for modelling have coarse resolutions (i.e., km), hence they do not have the precision to represent the full range of conditions within each grid cell. There may be smaller scale effects from other factors (e.g., topography, drainage) that make the condition of an area within one grid cell favourable for wiregrass, but these effects do not show up using the large-scale data. Second, sampling bias may have affected the predictive performance of the model. Sampling bias is often the reality in presence-only data (Phillips *et al.* 2009; Guillera-Arroita *et al.* 2015) and needs to be corrected to improve the predictive performance of models (Phillips *et al.* 2009). However, correcting for sampling bias does not entirely solve its effects on the performance of MaxEnt models (Syfert *et al.* 2013). Third, there may be some other causal predictor variables that were not used in the process, e.g. disturbance. Disturbances have been shown to affect the distribution (Wapstra *et al.* 2003) and abundance (Stuwe and Mueck 1990; Tolhurst 2003; Penman *et al.* 2009) of wiregrass, and may have a potential impact on the suitability of habitat for wiregrass.

The distribution of wiregrass in areas that were predicted as unsuitable may also suggest that wiregrass is a hardy species that can tolerate unfavourable conditions. Wiregrass occupies a wide range of habitats – in moist and dry areas (Ashton 2000; Penman *et al.* 2009), from sea level to the sub-alps (Willis 1970), in open and shaded areas (Ashwell 1985; Buckley 1993; Ashton 2000). This suggests that wiregrass can adapt to contrasting environments, and may even persist in unsuitable or stressful ones. A caveat here is that the binary classification of suitable or unsuitable habitats is based on an arbitrary cut-off, which means that the unsuitable areas where wiregrass occurs may not necessarily be unsuitable for wiregrass.

Wiregrass distribution under future climate

Since the distribution of wiregrass is most strongly associated with climate, future climate change is predicted to have a substantial impact on wiregrass distribution. Our results suggest that the area of suitable habitat for wiregrass will contract as temperature variation increases under climate change (i.e. annual mean temperatures outside the 10°C to 16°C range), drought becomes more severe (precipitation of driest month falling below 10mm), and rainfall decreases in the warm season. The distribution of wiregrass is also predicted to shift south (towards higher latitudes) with considerable reduction of climatically suitable habitat by 2100, and a possible increase in highly suitable habitats in the southern part of the range (Tasmania). Plant species shifting their ranges in different directions have already been reported in response to climate change (Parmesan 2006; Chen *et al.* 2011; Lenoir and Svenning 2015) and further range shifts are expected under future climate scenarios. Moreover, these range shifts are also associated with local extinctions (Wiens 2016). The predicted loss of suitable habitats in the northern-most part of the range for wiregrass suggests the possibility of local extinction in this part of its range. Climate-related local extinctions have already been reported for several plant species (Wiens 2016). Range shifts and associated local extinctions are two of the possible impacts of climate change on wiregrass distribution.

The predicted decline of suitable habitat may also mean a decrease in the flammability risk associated with wiregrass abundance under future climate scenario, if the abundance of wiregrass varies with habitat suitability (Whittaker 1975; Hengeveld and Haeck 1982; Weber *et al.* 2017). However, there is a need to investigate how the abundance of wiregrass would vary with the suitability of its habitat and also within areas of highly suitable habitat because site-specific factors can also influence abundance (see Chapter 3 and 4; Cadiz *et al.* 2020, 2021). A highly suitable habitat does not necessarily support high species abundance (Adhikari *et al.* 2018; Dallas and Hastings 2018). Furthermore, factors affecting distribution are not necessarily the factors driving local abundance because environmental factors may have differential effects on distribution and abundance (Duff *et al.* 2011; Tanner *et al.* 2017; Cadiz *et al.* 2020).

Limitations

Since this is a correlative study, it should be noted that the significant correlation of factors with wiregrass distribution does not necessarily indicate causal relationship. In addition, these factors were highly correlated with the excluded variables. Further, there is an inherent limitation of the predictive performance of models based on presence-only data (Elith *et al.* 2006; Penman *et al.* 2010) hence caution must be exercised in interpreting the results in this study. In addition, my analysis did not include the possible effect of disturbances (e.g., fire, logging), and the model also assumed that land use will be the same. Disturbances, particularly fires (Chitale and Behera 2019; Magadzire *et al.* 2019) and land use changes (Taylor *et al.* 2012; Ramachandran *et al.* 2020) have the potential to impact on habitat suitability and may significantly contribute to the contraction or expansion of the future distribution of wiregrass.

CONCLUSIONS

Wiregrass distribution was found to be strongly explained by five climatic factors and soil pH, suggesting that future changes to climate and soil chemical properties could significantly alter the distribution of wiregrass. Where there are associated changes in abundance with the altered future distribution, wiregrass may also influence community scale flammability. A high concentration of areas of highly suitable habitat for wiregrass is found in the southern portion of its range, particularly in the state of Victoria. These areas of highly suitable habitat are predicted to decrease in Victoria under future climate, contracting towards the southern part of the range but increase in Tasmania. An understanding of the factors associated with the distribution of wiregrass is important as this species has a disproportionate impact on forest flammability.

3 Environmental factors associated with the abundance of forest wiregrass, *Tetrarrhena juncea,* a flammable understorey grass in productive forests

Published: Cadiz et al (2020) Australian Journal of Botany 68(1): 37-48

https://doi.org/10.1071/BT19112

ABSTRACT

When flammable plant species become dominant, they can influence the flammability of the entire vegetation community. Therefore, it is important to understand the environmental factors affecting the abundance of such species. These factors can include disturbances such as fire, which can promote the dominance of flammable grasses causing a positive feedback of flammability (grass/fire cycle). We examined the potential factors influencing the abundance of a flammable grass found in the understories of forests in south-east Australia, the wiregrass *Tetrarrhena juncea* R.Br. When wiregrass is abundant, its structural characteristics can increase the risk of wildfire ignition and causes fire to burn more intensely. We measured the cover of wiregrass in 126 sites in Mountain Ash forests in Victoria, Australia. Generalized additive models were developed to predict cover against climatic and site factors. The best models were selected using an information theoretic approach. The statistically significant factors associated with wiregrass cover were annual precipitation, canopy cover, disturbance type, net solar radiation, precipitation seasonality and time since disturbance. Canopy cover and net solar radiation were the top contributors in explaining wiregrass cover variability. Wiregrass cover was predicted to be high in recently disturbed areas where canopy cover was sparse, light levels high and precipitation low. Our findings suggest that in areas with wiregrass, disturbances such as fire which reduce canopy cover can promote wiregrass dominance, which may in turn increase forest flammability.

INTRODUCTION

The influence of species on the emergent properties of an ecosystem is often proportional to their abundance (Parker et al. 1999). In fire-prone landscapes, such as in Australia, species within vegetation communities are fuels for wildfires (Murphy et al. 2013; Duff et al. 2017) and the traits of each species combine to influence flammability at landscape scales (Schwilk 2003; Schwilk and Caprio 2011; Zylstra et al. 2016; Tumino et al. 2019). When a flammable species becomes abundant, it can increase the flammability of an entire vegetation community (Gill and Zylstra 2005; Zylstra 2011; Schwilk and Caprio 2011) by contributing a disproportionate amount to the total fuel load or by altering structural characteristics of the vegetation community such as increasing fuel continuity (Brooks et al. 2004; Berry et al. 2011). However, the abundance of flammable species may not increase flammability of vegetation community if fuel aeration is substantially decreased with increased packing ratio or bulk density (van Wilgen and Richardson 1985; Scarff and Westoby 2006; Schwilk 2015; Fraser et al. 2016).

An example of an individual species that has become dominant and altered the flammability of a vegetation community is the invasive shrub *Lantana camara* L. in the dry rainforest of north-eastern Australia. This species increases the continuity of fuel in the understorey, consequently increasing the potential intensity and extent of fires that occur (Berry et al. 2011). Similarly, the dominance of the invasive African gamba grass *Andropogon gayanus* Kunth in northern Australia savanna causes higher intensity fires by increasing the fuel load seven-fold in comparison to natural fuels (Rossiter et al. 2003; Setterfield et al. 2010). In some instances, a positive feedback can be created where fire promotes the abundance of a flammable grass species, which in turn facilitates further fires (D'Antonio and Vitousek 1992; Rossiter et al. 2003). This process, known as a grass/fire cycle, has been observed in different ecosystems around the world (D'Antonio and Vitousek 1992). A contrasting example is the invasive succulent *Carpobrotus edulis* (L.) N.E. Br. in California (Zedler and Scheid 1988; D'Antonio et al. 1993) which has a high water content and low flammability, hence, reduces the flammability of the vegetation community when abundant (Brooks et al. 2004).

To better understand the drivers of flammability, it is important to understand the factors influencing the abundance of species that can have an effect on the flammability of plant communities. Many environmental factors are potentially important determinants of plant abundance, including precipitation, temperature, solar radiation, canopy cover and disturbance (Figure 3.1). For example, studies have shown that in drier areas, drought-intolerant species are rare while drought-tolerant ones are generally abundant (Gaff and Latz 1978; Badano et al. 2005). Similarly, in warmer areas, cold-adapted plants are rare while thermophilic species are generally abundant (Vesperinas et al. 2001; Kullman 2008). Shade-tolerant species are also reported to dominate under deep shade where shade-intolerant ones are generally absent (Chávez and Macdonald 2010).

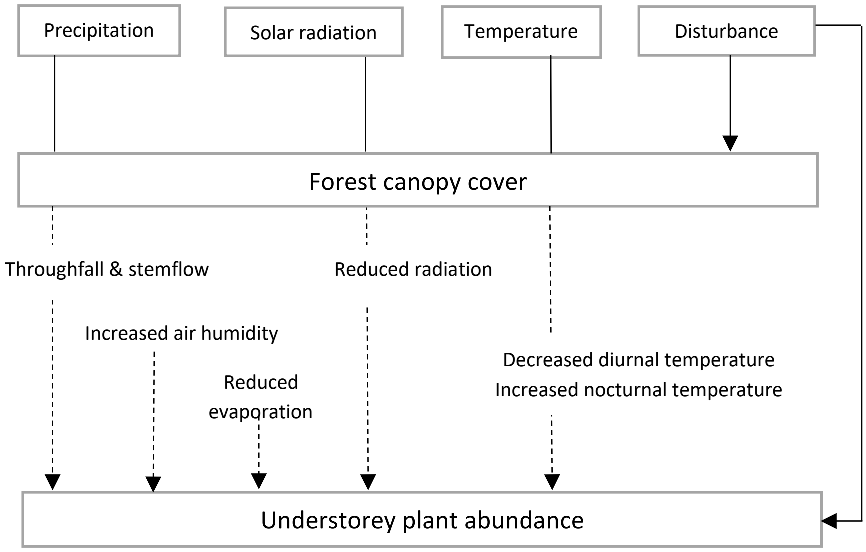


Figure 3.1 Canopy cover alters the micro-climate in the forest understorey affecting plant abundance. (In this study, canopy cover is the canopy provided by the vegetation from approximately 1.6m and above.) Broken lines represent the conditions as affected by canopy cover. Disturbance (e.g. fire, logging) may directly affect both canopy cover and understorey plant abundance.

In multi-strata forest systems, canopy cover plays a role in regulating plant abundance by modifying the factors that directly drive plant abundance (Figure 3.1). For example, light and water (from precipitation) are intercepted by the canopy (Valladares et al. 2016) resulting in a decrease in the availability of these resources. Canopy shading also decreases diurnal temperature and increases nocturnal temperature (Jacobs et al. 1994; Niinemets and Valladares 2004), resulting in narrower daily temperature fluctuations than those in the open. Studies also have shown that air humidity is increased, and evaporation is decreased under the canopy (Chen et al. 1995; Holmgren et al. 1997). Canopy cover can change in response to other factors including forest disturbance (e.g. fire, logging), drought or disease. Disturbances by themselves can also directly affect plant composition and abundance through their effects on mortality of plant populations or as a cue for regeneration and germination (e.g. fire-induced seed germination) (Gill 1981). The role of past disturbance influencing species abundance directly and indirectly is also emphasised by the grass/fire cycle concept (D'Antonio and Vitousek 1992).

One understorey species in south-eastern Australia that reportedly increases in abundance after a fire disturbance is the native wiregrass (Stuwe and Mueck 1990; Penman et al. 2009). Wiregrass is a scrambling grass that can grow over rigid supports even up to 6 m high, and as such, it is likely to become a ladder fuel, increasing the vertical and horizontal continuity of the fuel bed. Wiregrass has been reported to have a strong influence on the overall flammability of the coastal and foothill forests in south-eastern Australia (Buckley 1993; Fogarty 1993) by increasing the continuity of the fuel bed when it is abundant. It can sustain fire within a vegetation community even at high levels of humidity and at much higher surface litter moisture contents than fire would usually be sustained (Buckley 1993). Presumably this is because wiregrass has an aerated and elevated structure with a high fraction of suspended dead material (Fogarty 1993), which has a lower moisture content than the fuel on the forest floor as suspended materials have a high degree of exposure to atmospheric drying. Wiregrass is observed to abound under canopy gaps, with higher light levels thought to be the responsible factor stimulating thick growth in gaps (Lamp et al. 2001). However, Ashwell (1985), in his study on wiregrass ecology in Mountain Ash-dominated (*Eucalyptus regnans* F. Muell.) forest, could not confidently conclude which abiotic variable - light or soil moisture – played a greater role in defining wiregrass abundance. Wiregrass occurs very frequently but at vastly different levels of abundance in

Mountain Ash-dominated forest, hence, this forest type provides an ideal environment to study wiregrass abundance.

In this study, we aimed to identify the key environmental factors influencing wiregrass abundance. We conducted field surveys of wiregrass abundance in Mountain Ash-dominated forest. We use our results to discuss the conditions under which wiregrass becomes abundant and the potential of wiregrass to initiate a positive flammability feedback loop akin to the grass/fire cycle.

METHODS

Study species

Wiregrass is a rhizomatous perennial native grass that flowers during the warmer part of the year (between November and April) (Walsh and Entwisle 1994). It assumes different structural forms when abundant such as thick swards and stook-like structures climbing up to 6 m high over rigid supports like tree trunks, tree ferns, tree stumps, and shrubs. It is often found in low abundances but can exhibit prolific growth and become the dominant understorey species in certain areas. Wiregrass is found in the states of Victoria, Tasmania, New South Wales, Queensland, and South Australia. It occurs in a wide range of environmental conditions, from dry to moist habitats, and occurs from sea level to the sub-alps (Willis 1970; Ashwell 1985; Ough and Ross 1992).

Study area and site selection

The study was conducted in Mountain Ash (*Eucalyptus regnans* F. Muell.) forests in the Central Highlands region of Victoria, Australia. Mountain Ash forests occur in areas with deep, fertile soils and high rainfall (> 1,000 mm yr-1) (Ashton and Attiwill 1994). The overstorey is dominated by Mountain Ash trees but other eucalypt species including *E. cypellocarpa* L.A.S. Johnson and *E. obliqua* L'Hér are sometimes present (Ashton and Attiwill 1994). Common species in the understorey aside from wiregrass include *Pomaderris aspera* Sieber ex DC, *Olearia argophylla* F. Muell. ex Benth, *Dicksonia* *antarctica* Labill., *Cyathea australis* (R.Br.) Domin, *Correa lawrenciana* Hook., *Clematis aristata* R.Br. ex Ker Gawl., *Coprosma quadrifida* (Labill.) B.L.Rob., *Polystichum proliferum* (R.Br.) C.Presl and *Pteridium esculentum* (G.Forst.) Cockayne (Ashton and Attiwill 1994; Department of Sustainability and Environment 2004).

Fires are an important part of the lifecycle of Mountain Ash forests (Ashton 1981; Ashton and Attiwill 1994) and the subsequent regeneration pathway after high and low severity fires can be different (Ashton and Martin 1996). Where fire severity is high, both the overstorey and understorey are impacted, and dense regeneration of eucalypts from seed occurs, resulting in an even-aged stand (Ashton 1976). Where fire severity is low, the understorey and a few trees in the overstorey are impacted (Ashton and Martin 1996; Benyon and Lane 2013), and a multi-age forest could result (McCarthy and Lindenmayer 1998; Lindenmayer et al. 2000). Major wildfires have affected the study region, including those that occurred in 1939, 1983 and 2009 (Collins 2009). Selective harvesting (Griffiths 2001) and clear-fell logging (Florence 1996) have also been practised.

The study area was stratified based on time (in years) since last disturbance, type of disturbance (fire and logging), and aridity. Time since last disturbance was determined from mapped fire history (Department of Environment Land Water and Planning 2009, 2016a; b) and logging history (Department of Environment Land Water and Planning 2016c). The type of fire disturbance included a combination of low and high fire severities. Aridity index (Nyman et al. 2014) was used as proxy for topographic position and we aimed to locate sites across a range of aridity values (Cawson et al. 2018). Additionally, all sites were within 50-150 m of a road for accessibility, less than 30 degrees slope for safety, and at least 500 m apart when they had the same disturbance history. A total of 200 candidate plot locations within each stratification unit were selected through a spatial randomisation process.

We surveyed 126 sites out of the 200 candidate sites between April and June 2016. Table 3.1 outlines the different disturbance classes of the surveyed sites and the sample sizes for each disturbance class. The majority of our study sites were in the adolescent growth stage (9-35 yrs since fire or logging) (Cheal 2010). The sites were a subset of those surveyed by Cawson et al. (2018).

Table 3.1 Disturbance classes, time since disturbance and growth stages of the study sites, and their sample sizes.

Disturbance classes*	Time since disturbance* (years)	Growth stage (Cheal 2010)	Sample size (total n = 126)
2009 Fire	7	Juvenility	33
1983 Fire	33	Adolescence	20
1939 Fire	77	Maturity	33
2000-2010 Clearfell Logging	6-16	Adolescence	20
1990-1999 Clearfell Logging	17-26	Adolescence	11
1980-1989 Clearfell Logging	27-36	Adolescence	6
Long unburnt	100+	Maturity	3

*Department of Environment Land Water and Planning 2009, 2016a; b; c.

Field data collection

Wiregrass cover and canopy cover were assessed at each site along two 50-m transects oriented parallel and perpendicular to the slope. We used a line-point intercept method to measure cover along each transect (Elzinga et al. 1998) as the method provides higher precision than visual estimates (Godínez-Alvarez et al. 2009). Hits were recorded at 2 m intervals using a metal pin (1 m tall and 1.6 mm in diameter) oriented vertically; a hit was when the pin touches wiregrass at least once along its length. Wiregrass cover was computed as the total number of hits from the two transects divided by the total number of intervals from the two transects. Canopy cover was recorded at the same 2 m intervals along the transect using a vertical sighting tube (GRS Densitometer - Geographic Resource Solutions, Arcata, CA; Wilson 2011) and using a binary system of 'canopy' or 'sky' for each point. Measurements were taken from a height of approximately 1.6 m, thus canopy cover as used in this study encompassed any vegetation above that height. Canopy cover was computed as the total number of 'canopy' hits from the two transects divided by the total number of intervals from the two transects.

Aspect and elevation were recorded at each site. Aspect was converted to degrees from north to account for the effect of topography on microclimatic conditions. North-facing slopes in the southern hemisphere have greater light intensity, higher temperatures, and lower moisture availability than south-facing slopes (Swanson et al. 1988).

Environmental spatial data

We obtained precipitation and temperature variables from WorldClim 1 global coverage climate map (resolution = 0.5 minute of a degree, ~1 km) which uses long-term average climate data from 1960 to 1990 (Hijmans et al. 2005). The spatial resolution of this dataset is relatively coarse. However, the distances between our sites are generally more than 1 km, thus it should be suitable for representing broad macroclimatic patterns. Smaller scale effects were accounted for by the elevation and aspect variables as potential indirect measures of changes in temperature and moisture at finer scales.

We used the net total solar radiation derived from Nyman et al. (2014), which accounted for the effect of topography on radiation reaching the ground. Table 3.2 lists all the candidate predictor variables in this study.

Data processing and analyses

A variable reduction process was undertaken to reduce the confounding effect of collinear predictor variables. Pearson correlation coefficients between predictor variables were calculated (Appendix 1). When two variables had a correlation higher than 0.7 (Green 1979; Dormann et al. 2013), we retained proximal variable over distal, or direct variable over indirect, or resource variable over non-resource. Austin (2002) defines proximal and distal as “the position of the predictor in the chain of processes that link the predictor to its impact on the plant” – proximal being the more likely to be causal in determining plant responses. Direct variables are those with direct physiological effect on plants, e.g. temperature, as oppose to indirect variables, e.g. elevation (Austin 2002). Variables in bold in Table 3.2 were the final set of predictor variables after removing correlated variables.

Table 3.2 Potential predictors for the generalized additive modelling (GAM) process. Variables included in building the model after exclusion of highly correlated variables are in bold.

Variables	Units	Source
Annual mean diurnal range	degrees Celsius	WorldClim
Annual mean temperature	degrees Celsius	WorldClim
Annual precipitation	millimetres/year	WorldClim
Annual temperature range	degree Celsius	WorldClim
Aspect	degrees	Field measured
Canopy cover	%	Field measured
Disturbance type	none	Department of Environment Land Water and Planning 2009, 2016a; b
Elevation	meter	Field measured
Isothermality	%	WorldClim
Maximum temperature of warmest month	degrees Celsius	WorldClim
Mean temperature of coldest quarter	degrees Celsius	WorldClim
Mean temperature of driest quarter	degrees Celsius	WorldClim
Mean temperature of warmest quarter	degrees Celsius	WorldClim
Mean temperature of wettest quarter	degree Celsius	WorldClim
Minimum temperature of coldest month	degrees Celsius	WorldClim
Net solar radiation	MJ m^{-2} day^{-1}	Nyman *et al.* 2014
Precipitation of coldest quarter	millimetres	WorldClim
Precipitation of driest month	millimetres	WorldClim
Precipitation of driest quarter	millimetres	WorldClim
Precipitation of wettest month	millimetres	WorldClim
Precipitation of warmest quarter	millimetres	WorldClim
Precipitation of wettest quarter	millimetres	WorldClim
Precipitation seasonality	%	WorldClim
Temperature seasonality	degrees Celsius	WorldClim
Time since disturbance	years, log-transformed	Cawson *et al.* 2018

We fitted a quasi-binomial generalized additive models (GAM) of wiregrass cover against the final set of predictor variables to determine which variables explained the observed variability of wiregrass cover. GAMs were used as they fit data-defined splines and make no assumptions about the form of the relationships prior to fitting. GAMs were fitted using an information theoretic approach whereby the degrees of freedom available for each model term was set using a shrinkage approach. This reduces complexity of fitted relationships where there is limited statistical support. Where statistical support for inclusion was not significant, terms were excluded from the final model (in effect, a variable selection process). A maximum of four knots were allowed for each variable in fitting the GAMs. Models were fitted in R using the *mgcv* package (Wood 2011). The Shapiro-Wilks test was performed on the residuals of the model to check for normality of the distribution of residuals. We checked model performance by comparing fitted values against the observed values. We determined the relative importance of predictors by calculating the change in R-squared when each variable is added to the model that contains all the other variables.

All analyses were performed using R version 3.5.0 (R Core Team 2018).

RESULTS

Wiregrass was present in most of the study sites (115 sites out of 126), ranging in cover from 2% to 100% (mean = 43.9; sd = 30). Almost half (47%) of the study sites had a wiregrass cover of at least 50%, where wiregrass either formed a sward on the forest floor (Figure 3.2) or climbed over rigid supports (e.g. shrubs, tree trunks, tree ferns) up to 6 m (Figure 3.2). Canopy cover (i.e. the canopy provided by the vegetation from approximately 1.6m and above) in the study area ranged from 46% to 96% (mean = 76.9; sd = 12.2), where two-thirds of the study sites had a canopy cover of more than 75%. Some sites with a canopy cover in the higher range (> 90%) still supported relatively high wiregrass cover (at most 76% cover).

Figure 3.2 Wiregrass in the understorey of wet forests. Top photos: thick wiregrass swards covering the forest floor. Bottom photos: 'stooking' wiregrass, climbing through rigid support like tree trunks.

The model fitting process was able to create a GAM model that explained 37.7% of the variability in wiregrass cover. The parameters of the model are presented in Table 3.3. The model identified six significant variables that explained the variability in cover: annual precipitation, canopy cover, disturbance type, net solar radiation, precipitation seasonality, and time since disturbance. Canopy cover and net solar radiation were the top contributors of the model, with independent contributions of more than 20% of the R-squared (22% and 29%, respectively), while all the other variables contributed less than 10% each. Wiregrass cover is predicted to be relatively high in sites with relatively low canopy cover (Figure 3.3b), high net solar radiation (Figure 3.3d), lower annual precipitation with less variation (Figure 3.3a,c), and are recently-burnt (Figure 3.3c,f). The model tended to overpredict low wiregrass cover and underpredict high cover (Figure 3.4).

Table 3.3 Model parameters. Numbers for each predictor variable are the estimates and *t*-value (for parametric terms) or *edf* and *F* (for smooth terms). Significant predictor variables based on the fitted generalized additive model are marked with asterisk (p-values and significance code: 0 '***' 0.001 '**' 0.01 '*' 0.05).

Variables	Estimates or *edf*	*t*-value or *F*
Annual precipitation	0.783	1.106*
Canopy cover	1.232	5.630***
Disturbance type		
Fire (reference)	-0.1132	-0.915
Logging	-0.5537	-2.176*
Net solar radiation	1.136	6.211***
Precipitation seasonality	1.250	1.221*
Time since disturbance	1.435	3.513**
Adj R-sq	*0.392*	
Deviance explained	*37.7%*	

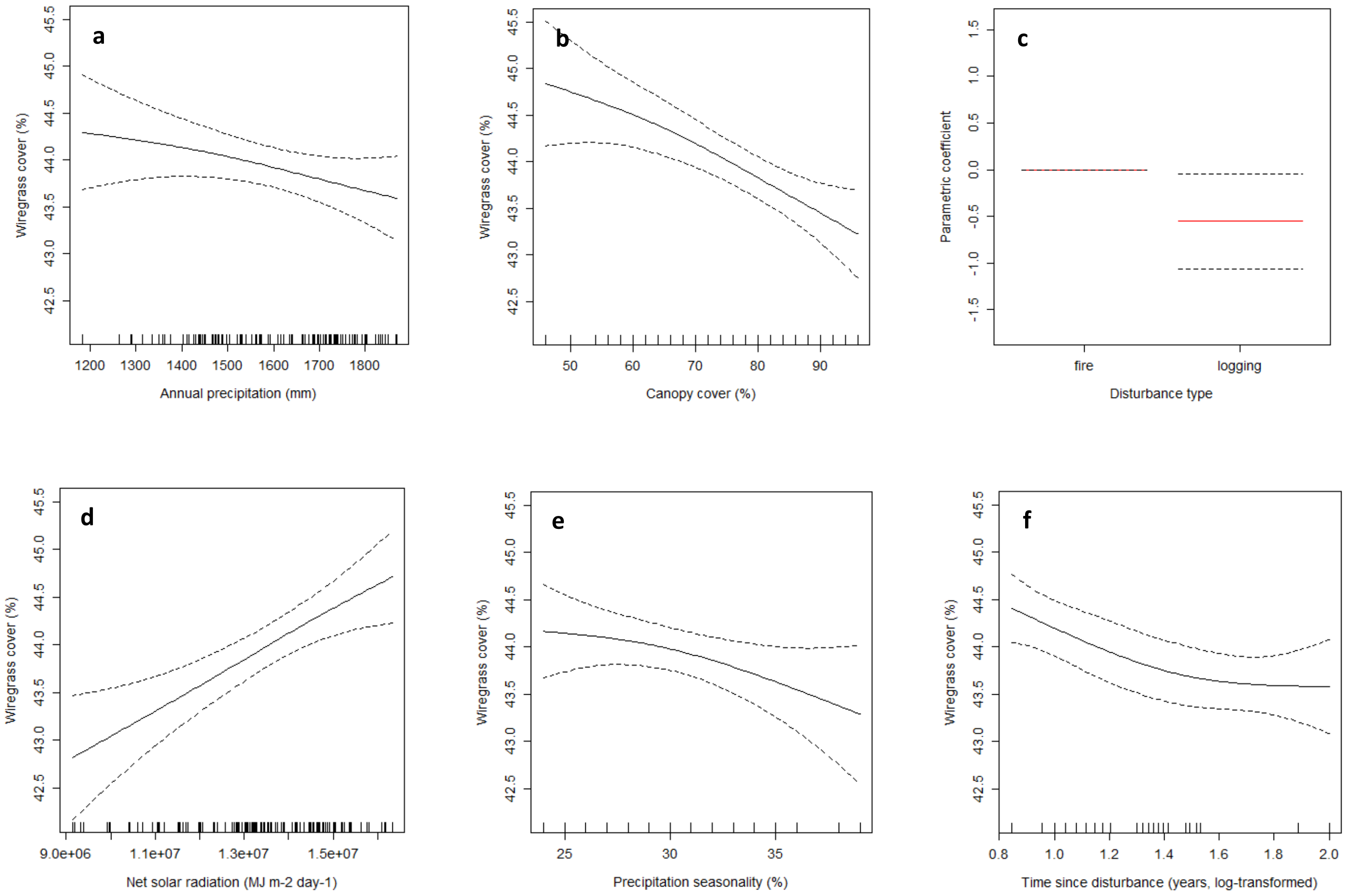


Figure 3.3 Partial plots of GAM fits for wiregrass cover against a) annual precipitation (mm), b) canopy cover (%), c) disturbance type, d) net solar radiation (MJ/m^{2}day), e) precipitation seasonality (%), and f) time since disturbance (years, log-transformed).

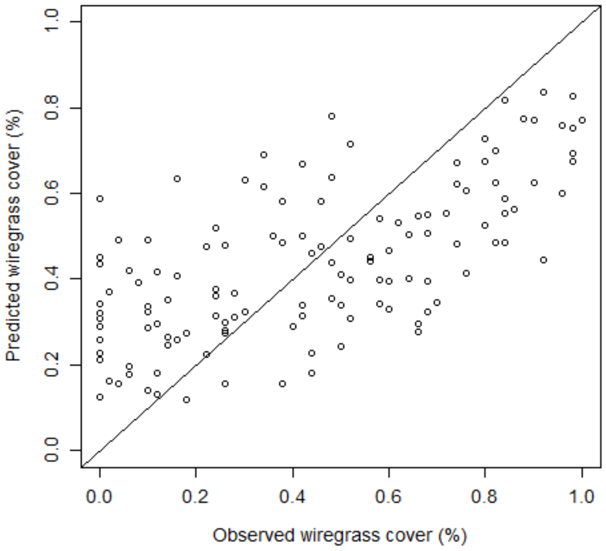


Figure 3.4 Plot of GAM fitted values of wiregrass cover against the observed values. The model tends to overpredict low wiregrass cover and underpredict high ones.

DISCUSSION

Environmental factors associated with wiregrass abundance

Low canopy cover and high net solar radiation are associated with high wiregrass abundance, suggesting that wiregrass can be considered as a gap or pioneer species. Canopy cover has a direct influence on resources (i.e. solar radiation and precipitation) reaching the understorey (Valladares et al. 2016) and it is likely that for this reason it was one of the two most important factors influencing wiregrass cover. Although such may be the case, net solar radiation reaching wiregrass in the understorey can differ between sites having the same canopy cover but different aspect (equator-facing vs pole-facing slope) (Swanson et al. 1988), hence the independent effect of net solar radiation from canopy cover on wiregrass cover. The variability of wiregrass cover in the understorey is likely to be a net response to a combination of factors shaped by the canopy cover. Stands with sparse canopies let more light and precipitation into the understorey than stands with dense canopies (Anderson et al. 1969; Chen et al. 1999), but the moisture will be reduced because of increased evaporation (Nyman et al. 2018). These conditions under sparser canopies correspond to higher wiregrass cover. This pattern is consistent with the results of Ashwell (1985) who found wiregrass was highly abundant in illuminated, drier areas. Further research is needed to decouple the effects of light and water (both influenced by canopy cover) on wiregrass growth and biomass to help us understand the individual role and interactive effects of these resources on wiregrass dominance.

Disturbance in general was associated with high wiregrass cover, suggesting that wiregrass can take advantage of disturbances to become dominant. Wapstra et al. (2003) observed that wiregrass distribution in Tasmania was more pronounced in greatly disturbed sites (disturbances include fire, logging and anthropogenic ones). Disturbance has been associated with native species becoming unusually dominant in their own range (Pivello et al. 2018), and also with exotic invasive species that dominate new areas (Sher and Hyatt 1999).

The influence of time since disturbance on wiregrass cover in the understorey is likely mediated by direct effects on competition and indirect effect via changes in canopy cover. During early post-disturbance, competition among species for space and resources is lesser as many species are eliminated (Sousa 1984), which means that species with the ability to reproduce asexually like wiregrass can quickly increase in abundance (Ashton and Martin 1996). Furthermore, resources (e.g. light) can increase where disturbances reduced the canopy cover. Consequently, wiregrass cover can become relatively higher in the recently-disturbed sites. Wiregrass cover did not continue to decline significantly as time since disturbance increased most likely because of declining number of stems per hectare in Mountain Ash forest as it ages (Ashton 1976). This decline in the number of stems per hectare allows gradual increase in light to the understorey. Wiregrass cover is likely to increase again in very old stands (~200 years) where light may have significantly increased (Ashton 1976).

Fire and logging disturbances differed in their effects on wiregrass cover most probably because of the differential degree of disturbance fire and logging had on the sites.

Logging disturbs both vegetation and soil (Murphy and Ough 1997; Lindenmayer and Ough 2006), whereas fire mainly disturbs the vegetation. Soil disturbance during logging operation may expose soil-stored seeds and rhizomes, which are then destroyed during the burning employed as part of the clear-fell logging procedure (Lindenmayer and Ough 2006). Consequently, wiregrass regeneration after clear-fell logging is potentially lower than after fire. Fire does not necessarily disturb the soil, and the smoke stimulates wiregrass seeds to germinate (Penman et al. 2008). This could explain relatively higher wiregrass cover in burnt than logged sites.

Our result suggests that climatic factors affect wiregrass abundance. Wiregrass cover was significantly correlated with both annual precipitation and precipitation seasonality, even though the data resolution was coarse. However, the precipitation variables were highly correlated with temperature variables, so it is unclear whether precipitation or temperature is more important to wiregrass cover. Whichever is the case, climate variables can be important determinants of wiregrass abundance.

An important biotic factor that may contribute to the remaining unexplained variance (> 50%) in wiregrass cover is herbivory, which we did not include in our study. Herbivores like wombat (*Vombatus ursinus* Shaw, 1800) (Ashwell 1985; Ashton and Chappill 1989), sambar deer (*Cervus unicolor* Kerr, 1972) (Forsyth and Davis 2011), eastern grey kangaroo (*Macropus giganteus* Shaw, 1790) and black wallaby (*Wallabia bicolor* Desmarest, 1804) (de Munk 1999) reportedly graze on wiregrass. It has been suggested that wombat abundance could have a considerable impact on wiregrass cover (Ashwell 1985; Ashton and Chappill 1989). Further research could consider the influence of herbivory on wiregrass abundance and structure.

Role of wiregrass in a positive fire-flammability feedback

Our results suggest that wiregrass has the potential to create a positive fire-flammability feedback in Mountain Ash forests, akin to the grass/fire cycle in other systems. The grass/fire cycle is based on several premises (D'Antonio and Vitousek 1992; Rossiter et al. 2003). Firstly, that grass dominance alters fuel characteristics leading to increased fire frequency, extent or intensity. Field studies by Buckley (1993) suggest that this is the case with wiregrass. When wiregrass is abundant, fires are more likely to ignite and spread at high surface fuel moisture contents, i.e. greater than 20% (Buckley 1993) when fires would otherwise self-extinguish (Cheney 1981). Another premise underpinning the grass/fire cycle is that altered fire regimes resulting from the abundance of particular grasses can create changes in tree cover. Altered fire regimes (i.e. increased fire frequency) in Mountain Ash forests can eliminate Mountain Ash from a site (Fairman et al. 2016). The extent that wiregrass abundance drives fire frequency in these forests is unclear. The final premise of the grass/fire cycle is that grass cover increases in the post-fire community. Our results show that wiregrass cover is higher in recently-burnt sites than long-unburnt ones, with fire disturbance likely acting as a stimulus for wiregrass growth. This evidence suggests that the grass/fire cycle may be applicable to wiregrass in Mountain Ash forests, but further research is needed to determine the importance of wiregrass abundance to fire frequency or extent in these forests.

Potential effect of climate change on wiregrass abundance

Fire frequency is hypothesized to increase under climate change (Pitman et al. 2007; Bradstock et al. 2014; Seidl et al. 2017) and precipitation is predicted to decrease in south-eastern Australia (Whetton 2011). Both these conditions could increase the abundance of wiregrass but that would also depend on the lower limit of moisture tolerance of wiregrass. Increased aridity may also reduce wiregrass abundance if moisture becomes a factor limiting wiregrass growth. Further study is needed to determine how wiregrass responds to drought, and how reduced canopy cover caused by disturbance interacts with impacts of low moisture on wiregrass.

CONCLUSION

Dominant species can strongly influence the flammability of vegetation communities, hence understanding the factors affecting the abundance of such species is important. Wiregrass, a species which increases the flammability of forest understories when it occurs abundantly, was found to increase in abundance in recently disturbed sites with reduced canopy cover, more light and lower precipitation. This suggests that disturbances such as fire that reduce canopy cover in sites where wiregrass is present can promote wiregrass dominance, which in turn increases flammability. This may create a positive flammability feedback.

4 Independent effects of drought and shade on growth, biomass allocation and leaf morphology of a flammable perennial grass *Tetrarrhena juncea* R.Br.

Published: Cadiz et al (2021) Plant Ecology 222(8): 877-895.

https://doi.org/10.1007/s11258-021-01148-y

ABSTRACT

Knowing the abundance of different plant species provides insights into the properties of vegetation communities, such as flammability. Therefore, a fundamental goal in ecology is identifying environmental conditions affecting the abundance of plant species across landscapes. Water and light are important environmental moderators of plant growth, and by extension, abundance. In the context of understanding forest flammability, the abundance of a flammable plant species in terms of its cover or biomass can shape the flammability of the whole vegetation community. We conducted a glasshouse experiment to determine the impact of drought and shade on growth, biomass allocation and leaf morphology of wiregrass, a rhizomatous perennial grass. When it is abundant, this species is known to contribute substantially to the flammability of eucalypt forest understories (via both ignitability and combustibility). Contrasting hypotheses in the literature predict that drought can have a weaker, stronger, or independent (uncoupled) impact on plant growth when light is limiting. We used a randomized complete block design with ten treatments from the combination of two water levels (drought, well-watered) and five light levels (100%, 80%, 60%, 40%, 20%). Drought and shade were found to have independent effects on wiregrass growth, biomass allocation, and leaf morphology, supporting the uncoupled hypothesis. Growth showed greater plasticity in response to drought, while biomass allocation and leaf morphology showed greater plasticity in response to shade. Our results suggest that wiregrass is more likely to be abundant in terms of its cover and biomass when water is not limiting. Under these conditions, the increased wiregrass abundance could create a window of increased flammability for the forest ecosystem.

INTRODUCTION

A fundamental goal in ecology is identifying environmental conditions that influence the abundance of plant species across landscapes (Crawley 1997). This is important because the contribution or effect of a species to ecosystem function and properties is often proportional to its abundance (Leibold 1995; Bradley 2016). Such is the case in flammable ecosystems where increased abundance (cover or biomass) of a species with highly flammable traits (e.g. very fine fuel leaves and high dead fraction) can increase the intensity of fires within the ecosystem due to changes in fuel load, fuel bed continuity and dead fraction (Rossiter et al. 2003; Brooks et al. 2004; Setterfield et al. 2010; Berry et al. 2011). Examples of species that alter the flammability of whole vegetation communities as they increase in abundance include the invasive gamba grass *Andropogon gayanus* Kunth in Northern Australia (Rossiter et al. 2003; Setterfield et al. 2010), the invasive shrub *Lantana camara* L. in dry rainforests in Queensland, Australia (Berry et al. 2011), and wiregrass *Tetrarrhena juncea* R.Br. in the eucalypt forests of south-eastern Australia (Buckley 1993). In these examples, plant abundance is considered in terms of plant cover or biomass (rather than number of individuals) as these metrics relate most to flammability. The total above-ground biomass of grasses, in particular, was found to be a strong driver of flammability (Rossiter et al. 2003; Setterfield et al. 2010; Simpson et al. 2016). In tropical forest-savanna transitions, flammable grass species was reported to have higher biomass in the open areas without tree canopy than in the shaded portions of the ecotone, resulting to suppression of fire at a particular point of the ecotone (Cardoso et al. 2018). Understanding the interplay between plant abundance and environmental factors will provide valuable insight into how ecosystem properties and function will change with changing environmental conditions.

Many factors in the environment can influence species abundance and their effects are not always straightforward. Biotic (e.g. herbivores, pests) and abiotic (e.g. climatic, edaphic, resource) factors can have both individual effects and interact with each other to influence species abundance (Bloom et al. 1985; Chapin et al. 1987; Smith and Huston 1989). Among these factors, water and light are resources that often limit plant growth (Daubenmire 1947; Gates 1980), and by extension, abundance or cover. The availability of these resources is spatially and temporally heterogeneous and, in forest systems, is largely influenced by canopy cover (Valladares et al. 2016), which in turn is influenced by disturbance (e.g. fire, logging, tree-fall) (Yamamoto 2000). This means that understorey vegetation can be subjected to variations in water and light availability through space and time, and this may lead to variations in plant productivity, plant community structure (Craine et al. 2012; Smith and Huston 1989) and dominance of understorey species (Chávez and Macdonald 2010; Halpern and Spies 1995; Veblen et al. 1977). Understanding how both drought and shade impact understorey plant performance independently or interactively will help us predict how forest disturbances and climate change, both of which alter resource availability (Sher and Hyatt 1999; Nicotra et al. 2010), might impact species abundance in terms of cover and biomass.

There are three hypotheses which predict the combined effects of limited availability of water (drought) and light (shade) on plant growth. The uncoupled hypothesis states that shade and drought have independent impacts on plant growth (Nobel 1999). The facilitation hypothesis proposes that shade reduces the impact of drought stress on plants, as shade results in lower temperatures and vapour pressure deficits which reduce plant water use and, therefore, demand for soil water (Holmgren et al. 1997). The trade-off hypothesis predicts that there is a trade-off between drought tolerance and shade tolerance because plants under shade will invest more in leaves to enhance light capture at the expense of reduced allocation to roots, consequently making the plant sensitive to drought (Smith and Huston 1989). Conversely, plants under dry conditions will invest more in roots to enhance water absorption, making them sensitive to shade. This trade-off in tolerance is argued to be the consequence of the trade-off in phenotypic adjustment under changing resource availability (Chapin et al. 1987; Smith and Huston 1989; Valladares et al. 2007; Couso and Fernández 2012). Empirical evidence does not consistently support a single hypothesis (Holmgren et al. 2012); therefore, the question of whether drought has independent, weaker, or stronger effects on plants under shade has not yet been resolved.

Phenotypic plasticity and functional traits can explain the ability of plants to grow and survive when resources become limiting (Amissah et al. 2015; Bradshaw 1965; Nicotra et al. 2010; Sultan 2000). Functional traits refer to morphological, physiological or phenological features that potentially affect fitness and that determine how plants respond to the environment (Pérez-Harguindeguy et al. 2013). Plasticity in functional traits can also enable plants to adjust to maximize acquisition of a limiting resource (Bloom et al. 1985; Chapin et al. 1987; Smith and Huston 1989). For example, increased allocation to roots (root mass fraction) under drought stress increases the surface area for absorption of water (Evans 1972; Aerts et al. 1991; Poorter et al. 2012), whereas increased leaf mass fraction, leaf area, leaf area ratio and specific leaf area under shade maximizes capture of light (Lambers et al. 2008; Loach 1967; Aerts et al. 1991). Plastic responses such as these are important in determining the persistence of plants under climate change where the availability of resources is altered (Nicotra et al. 2010). However, while plant responses to individual resource gradients are well studied, the responses due to interacting effects of two or more resources such as water and light are less understood (Holmgren et al. 2012).

In this study, we explored the combined effects of water and light on growth, and how it might influence abundance (cover and biomass) of wiregrass. Wiregrass is a C3 rhizomatous and stoloniferous perennial grass found in the understorey of forests in south-eastern Australia. It is an ecologically important species as it can strongly influence forest flammability (via both ignitability and combustibility) when it becomes abundant (Buckley 1993). A high cover of wiregrass not only increases the total fine fuel load but also the continuity of the fuel bed and dead fraction. Consequently, wiregrass enables fires to ignite and sustain at higher air humidity and surface moisture contents than would otherwise occur (Buckley 1993; Fogarty 1993). The fire risk associated with wiregrass is recognized in the coastal and foothill forests of south-eastern, Australia where burn prescriptions have been developed to cater specifically for this fuel type (Cheney et al. 1992; Buckley 1993).

Wiregrass has a broad habitat distribution (Ashton 2000; Ashwell 1985; Ough and Ross 1992; Penman et al. 2009; Willis 1970) and ranges from rare to dominant in abundance. This distribution in contrasting environments (i.e. in wet and dry forests, under shade and full light) strongly suggests that wiregrass has high phenotypic plasticity (Sultan 2000), and that trait plasticity may play a role in determining local abundance

(Cornwell and Ackerly 2010). A recent field study found that light and water were significantly associated with wiregrass abundance in terms of its cover (Cadiz et al. 2020). However, that study was unable to isolate the independent and interactive effects of these factors on wiregrass growth, which is needed to predict future changes in wiregrass abundance and its potential effects on forest flammability. To address this uncertainty, we tested the three competing hypotheses mentioned above through experimental manipulation with different levels of moisture and shade on wiregrass. The following specific questions were addressed: 1) What are the effects of drought and shade on wiregrass growth, biomass allocation, and leaf morphology? 2) Does wiregrass show plastic responses to drought and shade? We used the results to discuss how drought and shade influence the abundance of wiregrass in terms of cover. We also discuss the implications of our results for forest flammability and also the effect of climate change on wiregrass abundance.

METHODS

An experimental manipulation with two water levels and five light levels was conducted for 12 weeks inside a glasshouse to determine the effects of water and light on wiregrass growth, biomass allocation, and leaf morphology.

Study species

Wiregrass is a rhizomatous (stolons are also present) perennial understorey grass which flowers between November (late spring) and April (mid-autumn) (Walsh and Entwisle 1994). Wiregrass can form swards or climb up to six meters high over rigid supports like tree trunks, tree ferns, tree stumps, and shrubs (Cadiz et al. 2020). This scrambling grass thrives in both dry (Penman et al. 2009) and moist habitats (Ashwell 1985; Ashton 2000) in either open or shaded areas, and occurs from sea level to the sub-alpine regions of south-eastern Australia (Willis 1970) in places with different aspects, slope, and irradiance (Ashwell 1985; Ough and Ross 1992). Wiregrass belongs to tribe Ehrharteae and subfamily Ehrhartoideae of the Poaceae family.

Wiregrass cuttings were collected from a patch of one forest type, the Mountain Ash *(Eucalyptus regnans)* forests in the Central Highlands region of Victoria, Australia, to control for any population variation due to differences in forest type (Huang et al. 2008). Stem cuttings of approximately 100 mm long with at least one node were planted individually in propagation tubes (40 x 40 x 80 mm) filled with potting mix. The potting mix was composed of 1 part washed coarse sand and 7 parts medium pine bark, Macracote Colonizer Plus (Red) slow release fertilizer (N:P:K 15:3:9, plus trace elements) at a rate of 4 kg m-3, a soil wetter SaturAid (1.5 kg m-3), and dolomite lime (1 kg m-3). Field soil was not included in the mix to prevent the introduction of any soil pathogens into the nursery where the experimental study was conducted. The stem cuttings were placed outside the glasshouse but in a shaded area within the nursery of the University of Melbourne Burnley campus in Victoria, Australia until they initiated tillering and grew new shoots and roots (i.e. vegetative growth stage). We were most interested in the vegetative growth stage since this contributes greatly to the biomass and abundance of this flammable grass in forests. The growing cuttings were transplanted to bigger pots (140 mm diameter, 1.9L euro pots, Garden City Plastics) before the experiment, and then moved inside a glasshouse for one to two weeks for acclimation before the start of the experiment.

Experimental Design

There were two watering treatments in this experiment: well-watered (W) and drought (D). Well-watered plants were watered to pot capacity three times a week (Monday, Wednesday, Friday). The well-watered treatment is an optimal condition in our experiment which reflects natural conditions where wiregrass grows in wet forests. The drought treatment follows the protocol employed by Farrell et al. (2017) in investigating the effect of drought stress in plants. Plants in the drought treatment were watered to pot capacity only when the soil water content in the pot reached 5-10% above the permanent wilting point (PWP). PWP was 7.9% of the water-holding capacity (WHC = 54% w/w) of the potting mix or 4.3% soil water content (Richards et.al., 2017). Soil water content under drought treatment was monitored gravimetrically (Farrell et al. 2017). Whenever the pot weight dropped to a weight within the range equivalent to having a pot soil water content of 5-10% above PWP, the plant was re-watered to pot capacity. Watering of the drought pots was done every 15 days on average (Appendix 3d).

The light treatments in the experiment were achieved by using shade frames covered on all sides with shade cloth of different densities (Amzad Hossain et al. 2009; Maguire and Kobe, 2015; Wu et al. 2017; Zervoudakis et al. 2012) that allowed different amounts of light to pass through. Wiregrass is known to occur in open areas like forest gaps (Ashton 2000) as well as in forest understories with varying canopy cover. The vegetative cover above 1.5 m in wet eucalypt forests (where we collected the wiregrass planting material) is highly variable, ranging from 46 to 96% (Cadiz et al. 2020). Vegetative cover in wet eucalypt forests has been found to intercept approximately 90% of the total incoming solar radiation (Burton et al. 2019), while radiation interception in the more sparsely canopied dry eucalypt forests is lower (Pickering et al. 2021). In this experiment, we created relative light intensities spanning a range of conditions that might occur in both wet and dry eucalypt forests: 100%, 80%, 60%, 40%, and 20%. Shade frames were constructed out of PVC pipes (1.5m length x 1m width x 1m height), with three shade frames for each of the light levels. The 100% light level was the ambient light of the glasshouse, so this was achieved with a shade frame without shade cloth. The other relative light intensities were achieved using shade cloth mounted on all sides of the shade frames except the bottom. The relative amount of light passing through the shade clothes was specified by the manufacturer and verified using a light meter to determine the actual amount of light allowed by the shade cloth frames (Table 4.1). All shade frames were placed on top of mesh benches allowing complete air flow around the pots.

Table 4.1 Light treatments and the corresponding amount of light passing through the shade cloths used as determined by the shade cloth manufacturer and actual light meter readings

	Light treatment				
	100%	80%	60%	40%	20%
Manufacturer label	--	80-84%	--	40-50%	30%
Light meter reading	--	75-85%	51-61%	50-52%	11-32%

The study employed a randomized complete block design. Five replicates were randomly assigned to each treatment combination (one plant = one replicate) in each block, totalling 15 replicates per treatment combination. One hundred and fifty plants were used in total (5 light levels x 2 water levels x 3 blocks x 5 replicates). The ten treatment combinations (two water levels and five light levels) were randomly arranged within each of the three blocks inside the glasshouse. The blocking factor was the different locations inside the glasshouse.

The experimental manipulation was conducted from March to June 2018, coinciding with a time of year when wiregrass has been reported to exhibit a growth flush (during late autumn) (Ashwell 1981). Throughout the experiment, the average glasshouse temperature ranged between 18-26°C, which was within the range of temperatures where wiregrass is known to thrive in the natural environment (Willis 1970; Ashwell 1985; Fogarty 1993; Ashton 2000; Penman et al. 2009).

Trait measurements

A range of traits were measured (Table 4.2). Growth was measured by tiller growth rate, total live biomass, and the proportions of tillers that were live and dead. It was assumed that growth rate and total live biomass correlate with cover and biomass at field-scales, while the live and dead biomass proportions give an indication of dead fraction, which is important to flammability (e.g. plants with a higher dead fraction pose a greater fuel hazard) (Gould et al. 2011). Biomass allocation to root, stem and leaves were also determined because they have implications for water absorption, water transport and light capture, respectively, and can be highly plastic across water and light availability (Poorter and Nagel 2000; Poorter et al. 2012; Pérez-Harguindeguy et al. 2013). Leaf morphological measures, i.e. leaf area, leaf area ratio, specific leaf area, were also included as they influence light capture and can plastically adjust to different light levels (Rozendaal et al. 2006; Pérez-Harguindeguy et al. 2013).

Table 4.2 Descriptions and equations of growth, biomass allocation, and morphological variables assessed in wiregrass grown under varying levels of light and water

Variables	Measured from	Calculation formula
Growth:		
1. Tiller growth rate	Marked tiller	(final length - initial length) / (t2 - t1); *t1* and *t2* are dates when initial and final length were measured, respectively
2. Total live biomass	Whole plant	leaf dry wt + stem dry wt + root dry wt
3. Live biomass proportion	Whole plant	total live biomass / (total live biomass + total dead biomass)
4. Dead biomass proportion	Whole plant	total dead biomass / (total live biomass + total dead biomass)
Biomass allocation:		
5. Leaf mass fraction	Whole plant	leaf dry wt / total live biomass
6. Stem mass fraction	Whole plant	stem dry wt / total live biomass
7. Root mass fraction	Whole plant	root dry wt / total live biomass
Leaf morphology:		
8. Leaf area	Marked tiller	--
9. Leaf area ratio	Marked tiller	total leaf area / total biomass
10. Specific leaf area	Marked tiller	leaf area / leaf dry wt

One tiller per replicate was marked at the beginning of the experiment for the measurement of tiller length, leaf area, leaf area ratio, and specific leaf area (Table 4.2). All the other measurements were from the whole plant.

The experiment was conducted for 12 weeks including the period of the late-autumn growth flush of wiregrass, which reportedly lasts for 8 weeks (Ashwell 1981). All plants were harvested, and the leaves, stem and roots were separated after 12 weeks. Roots were washed with water to completely remove any remaining potting mix. Leaves, stems and roots were oven-dried at 70-80°C until weight was consistent and dry weights were recorded. Marked tillers were processed separately to measure final tiller length and leaf area. Leaf area was measured using a LI-COR LI 3100C Area Meter with leaves mounted with transparent tape on transparent plastic sheets to make sure that the blades were completely flattened before passing them through the leaf area meter.

Dry weights, tiller length and leaf area measurements were used to calculate trait values (calculation formulas in Table 2). The phenotypic plasticity index (PI) of wiregrass to water and light treatments was calculated separately for each trait. In this study, the PI was used to compare the response of each variable to water versus light treatment, and not to compare the response of all variables with each other. PI was calculated as the difference between the maximum mean value and the minimum mean value divided by the maximum mean value, PI = (max - min) / max, following Valladares et al. (2000a; 2000b), who also used this plasticity index to examine the plastic response of different variables to light treatments. We are using this PI formula as it is simple and widely used.

Data analyses

Two-way analysis of variance (ANOVA) was employed to examine individual and combined effects of water and light levels. Parametric assumptions were checked using Shapiro-Wilk's test (for normality of residuals) and Bartlett's test or Levene's test (for equality of variances). When residuals were not normally distributed and/or treatment groups were heteroscedastic, the response variables were transformed using the function *transformTukey* of the *rcompanion* package (Mangiafico 2018) in R Programming (R version 3.5.0) (R Core Team 2018) to enhance normality of residuals and homoscedasticity among treatment groups. The function *transformTukey* determines the kind of data transformation needed to produce more normally distributed residuals by choosing the lambda value that maximizes the Shapiro-Wilk's *W* (Mangiafico 2018).

Where there was no significant interaction, significant differences among means were compared using post-hoc analysis within light or water treatments. Tukey's HSD (parametric) or Dunn's test (non-parametric) was used when comparing light treatment groups. For Dunn's test, we used Bonferroni correction for multiple testing; Tukey's HSD already accounts for the issue of multiple comparisons. T-tests (parametric) or Wilcoxon rank sums tests (non-parametric) were used when comparing water treatment groups.

All analyses were performed using R version 3.5.0 (R Core Team 2018).

RESULTS

Effects of drought and shade

Wiregrass exhibited differences in responses across all water and light treatments (Appendix 3a, 3b, 3c). Drought and shade had no significant interaction effects on any traits (Table 4.3). There was also no significant block effect, except for a marginal effect on leaf area ratio ($p = 0.0265$). The following sections present only the main (independent) effects of drought and shade on growth, biomass allocation, and leaf morphology of wiregrass.

Growth

Drought had statistically significant effects on all growth variables (Table 4.3). Drought significantly decreased tiller growth, total live biomass and live biomass proportions, but significantly increased the proportion of dead biomass (Figure 4.1). The average tiller growth rate dropped by at least half the rate of well-watered plants across all light levels (Figure 4.1A). Total live biomass was reduced to approximately one-third the biomass of well-watered plants – from 26.4 to 9.0 g (Figure 4.1B). The proportion of live biomass was lower by 17% on average under drought than that of the well-watered plants (Figure 4.1C). Furthermore, the proportion of dead biomass of droughted plants was three times higher than that of well-watered plants (Figure 4.1D). Live and dead biomass proportions in droughted plants showed higher variation across the five light levels than for well-watered plants (Figures 4.1C and 4.1D).

Table 4.3. Summary of the ANOVA results and plasticity indices (PI) of the growth, biomass allocation and leaf morphological factors of wiregrass as affected by water and light. PI values in **bold** are averages of the variable groups

Traits	F and its significance (***: $p \leq 0.001$; **: $p \leq 0.01$; *: $p \leq 0.05$; ns: $p > 0.05$)				Phenotypic plasticity index (PI)	
	Water (W)	Light (L)	Block	W x L	PI water	PI light
Growth					***0.53***	***0.30***
1. Tiller growth rate	114.476***	7.572***	0.762 ^{ns}	0.786^{ns}	0.58	0.48
2. Total live biomass	386.319***	0.402^{ns}	1.561 ^{ns}	1.991^{ns}	0.66	0.20
3. Live biomass proportion	157.332***	3.075*	0.935 ^{ns}	1.114^{ns}	0.17	0.09
4. Dead biomass proportion	138.327***	3.273*	1.491 ^{ns}	1.442^{ns}	0.72	0.41
Biomass allocation					***0.10***	***0.21***
5. Leaf mass fraction	0.556^{ns}	9.382***	2.286 ^{ns}	1.432^{ns}	0.08	0.29
6. Stem mass fraction	5.858*	0.578^{ns}	0.990 ^{ns}	0.967^{ns}	0.05	0.07
7. Root mass fraction	12.050***	4.423**	0.092 ^{ns}	0.368^{ns}	0.16	0.28
Leaf morphology					***0.30***	***0.41***
8. Leaf area	74.339***	11.947***	1.811 ^{ns}	0.843^{ns}	0.47	0.53
9. Leaf area ratio	23.186***	8.374***	3.730*	1.549^{ns}	0.35	0.49
10. Specific leaf area	6.802*	14.299***	2.123 ^{ns}	2.099^{ns}	0.07	0.20

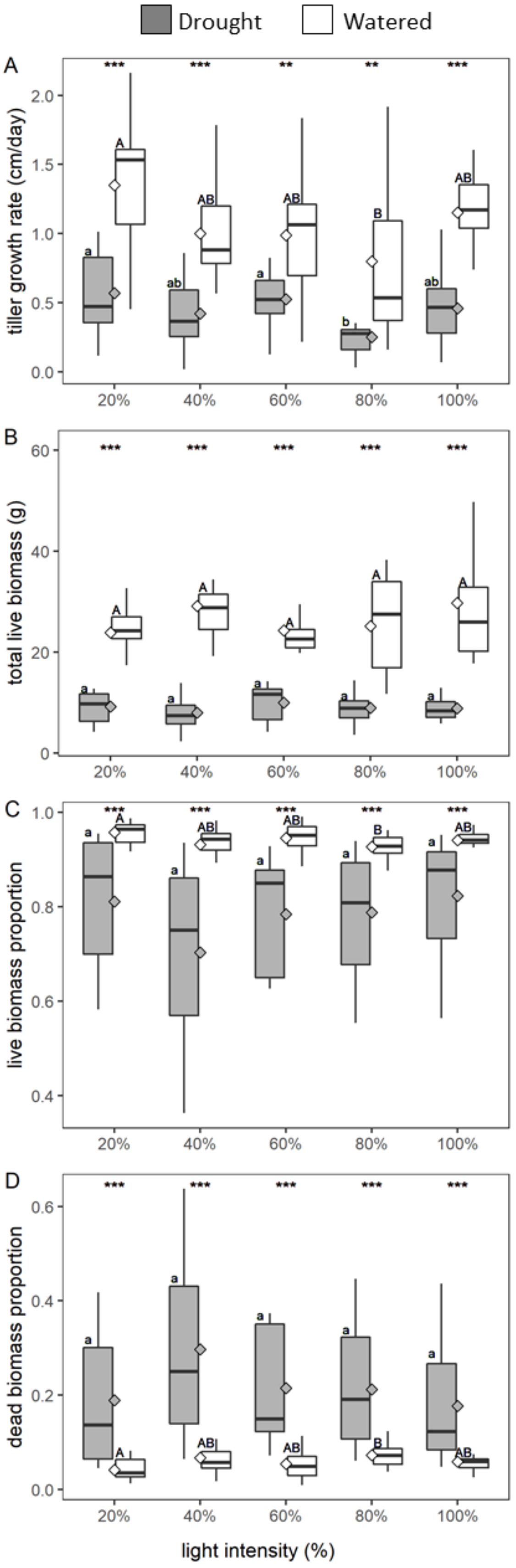


Figure 4.1 Effect of drought and shade on growth (A. tiller growth rate; B. total live biomass; C. live biomass proportion; D. dead biomass proportion) on wiregrass. Significance between drought and well-watered plants at the same light level is indicated on top in asterisk (***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$). Significance between light levels within each water group is indicated in letters ($p < 0.05$). Diamond shapes represent group means.

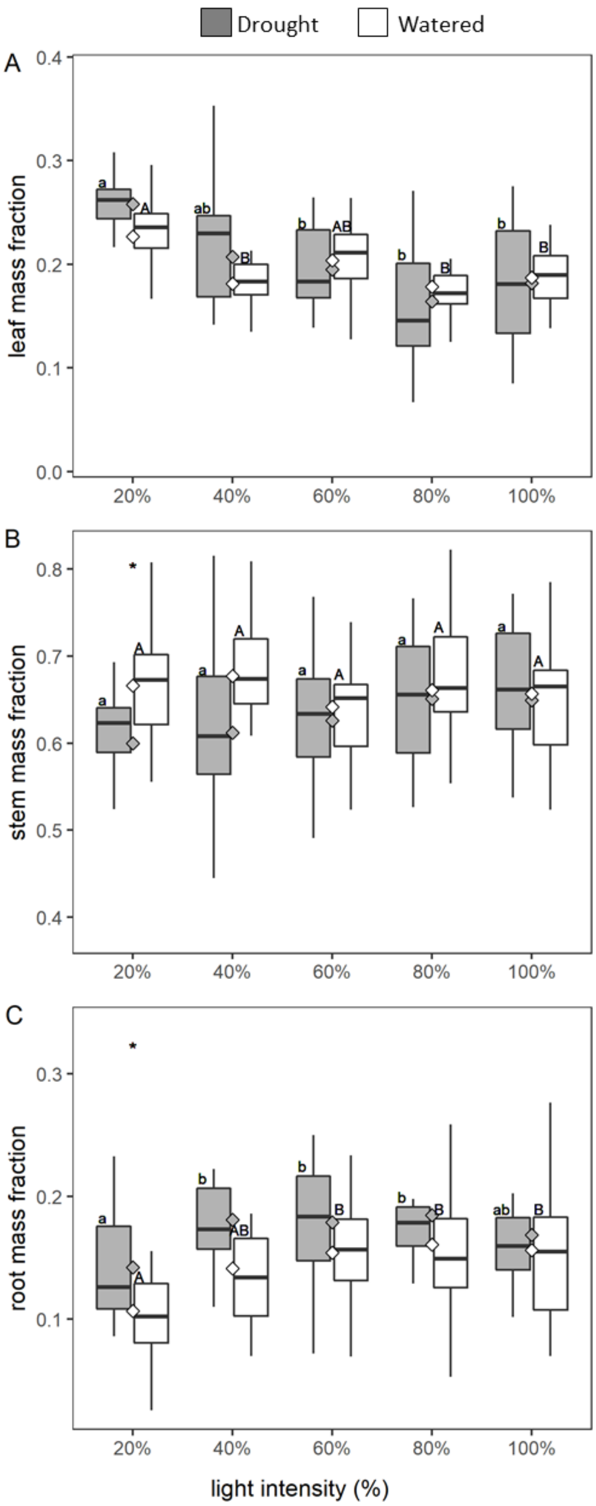
Overall, light treatments had statistically significant effects on tiller growth and the proportion of live and dead biomass, but not total live biomass (Table 4.3). Comparisons between individual treatments showed that growth did not significantly differ statistically between full light (100%) and the shade treatments (20-80%) but there were significant effects among the shade treatments (Figure 4.1). First, significantly higher tiller growth rate was observed at deep shade (20% light) than at light shade (80% light) for both the well-watered and drought treatments (Figure 4.1A). Tiller growth rate increased from 0.252 to 0.571 cm/day under drought as the light level decreased, and from 0.800 to 1.35 cm/day under the well-watered treatment. Second, the well-watered wiregrass under deep shade had a significantly higher proportion of live biomass (3% higher) and a lower proportion of dead biomass (40% lower) than those under light shade (Figure 4.1C and 4.1D).

Biomass allocation

Drought had a significant effect on biomass allocation particularly stem and root mass fractions (Table 4.3). Further analysis showed that this significant effect was only evident at 20% light treatment (Figure 4.2B, 4.2C), where stem mass fraction decreased by a tenth while root mass fraction increased by a third (p-values < 0.05) under drought conditions.

Light treatments had significant effects on leaf and root mass fractions (Table 4.3). Deep shade (20% light) significantly increased leaf mass fraction by a third and decreased root mass fraction by a fifth on average relative to full light (Figures 4.2A, 4.2C). Further analysis comparing patterns of relative allocations to leaves and roots across light levels showed differences depending on water availability. When water was not limiting (well-watered), wiregrass invested significantly more biomass in leaves and lesser in roots between 20-60% light (Figure 4.3A). Whereas when water was limiting (drought), wiregrass invested significantly more biomass in leaves than in roots only when light was very limited (20% light only; Figure 4.3B).

Figure 4.2 Effect of drought and shade on: A. leaf mass fraction; B. stem mass fraction; and, C. root mass fraction of wiregrass. Significance between drought and well-watered plants at the same light level is indicated on top in asterisk (***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$). Significance between light levels within each water group is indicated in letters. Diamond shapes represent group means.



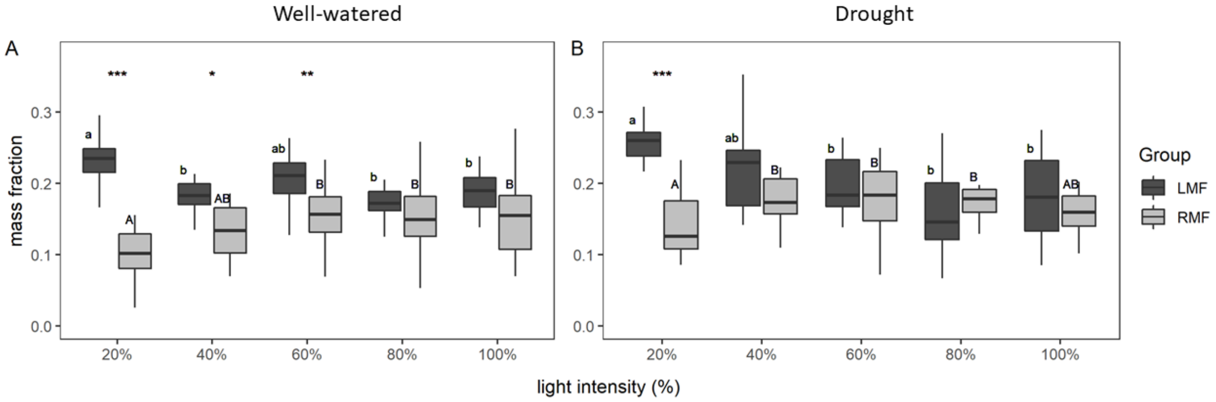
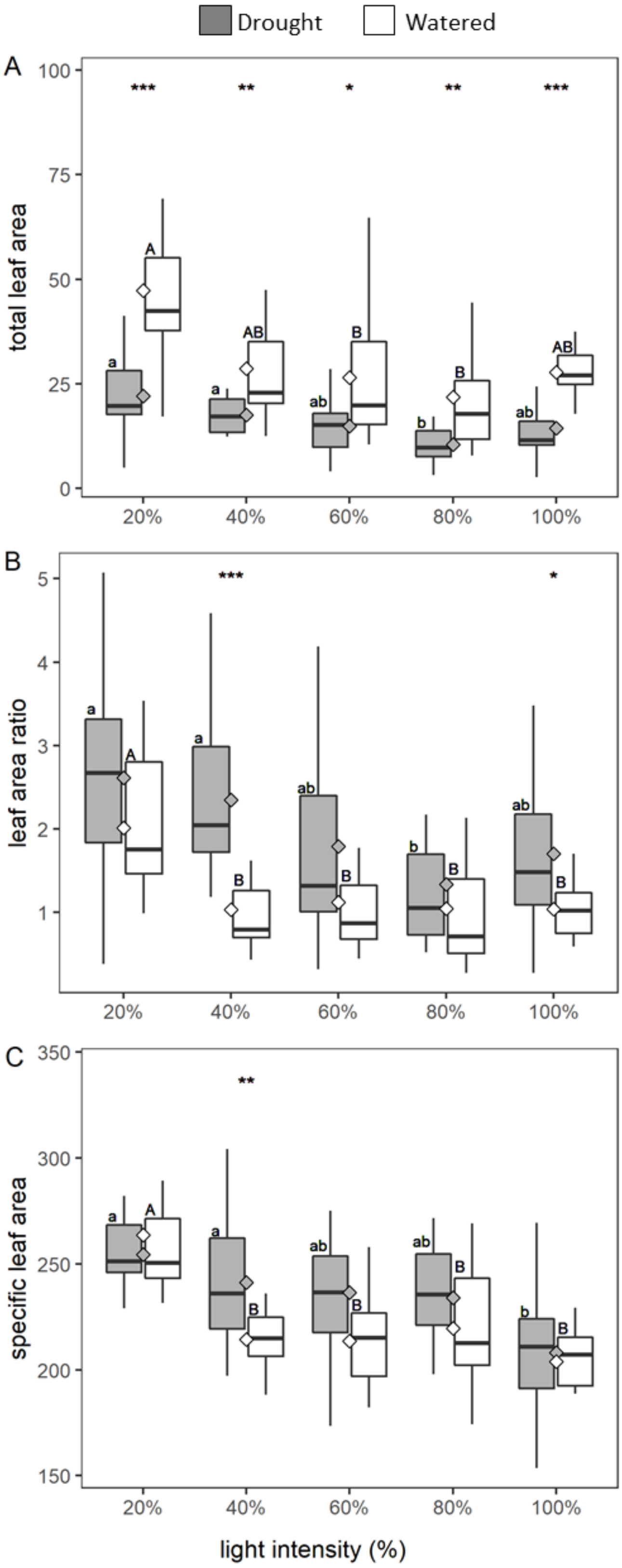


Figure 4.3 Biomass allocation in wiregrass (A. well-watered; B. drought). Significance between LMF and RMF at each light level is indicated on top in asterisk (***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$). Significance between light levels within each group is indicated in letters. LMF = leaf mass fraction; RMF = root mass fraction

Leaf morphology

Drought had statistically significant effects on all leaf morphology traits (Table 4.3). Leaf area was reduced by half under drought conditions (Figure 4.4A). Drought also increased the leaf area ratio and specific leaf area. However, within each light level, there were only significant differences in leaf area ratio between drought and well-watered plants for 40% and 100% light, with 128% and 63% higher leaf area ratio respectively in droughted plants (Figures 4.4B and 4.4C). Similarly, there was a significant difference in specific leaf area between drought and well-watered plants only for 40% light, with 13% increase in droughted plants.

Figure 4.4 Effect of drought and shade on: A. total leaf area; B. leaf area ratio; and, C. specific leaf area of wiregrass. Significance between drought and well-watered plants at the same light level is indicated on top in asterisk (***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$). Significance between light levels within each water group is indicated in letters. Diamond shapes represent group means.



Light treatments had statistically significant effects on all leaf morphology traits (Table 4.3). For total leaf area, a significant effect was evident within shade treatments only (Figure 4.4A), such as total leaf area at 20% light was more than double (110% and 116% in drought and well-watered treatments, respectively) the total leaf area at 80% light level. For leaf area ratio, it almost doubled in 20% light compared to 40-100% light under well-watered conditions (Figure 4.4B); whereas under drought conditions, a significant effect was evident within shade treatments only, where 20-40% light treatment significantly increased leaf area ratio by at least 77% relative to 80% light (Figure 4.4B). For specific leaf area, there was a statistically significant quarter increase in deep shade (20% light) relative to those in full light (Figure 4.4C).

Phenotypic plasticity

Wiregrass showed high variation among traits in the degree of phenotypic plasticity in response to light and water treatments (Figure 4.5, Table 4.3). Biomass allocation had the lowest overall PI average ($[0.10\ PI_{water} + 0.21\ PI_{light}] / 2 = 0.155$), while growth had the highest ($[0.53\ PI_{water} + 0.30\ PI_{light}] / 2 = 0.415$). Growth had the highest PI_{water} average among all trait groups while leaf morphology had the highest PI_{light} average (Table 4.3). The average PI for growth was higher in water than light, while the opposite was true for biomass allocation and leaf morphology (Table 4.3). Plasticity indices of individual traits were plotted as points in Figure 4.5, where traits plotted above the diagonal dotted line showed greater plasticity to water while traits plotted below the line showed greater plasticity to light. Hence, growth had greater plasticity in response to water, whereas biomass allocation and leaf morphology had greater plasticity in response to light.

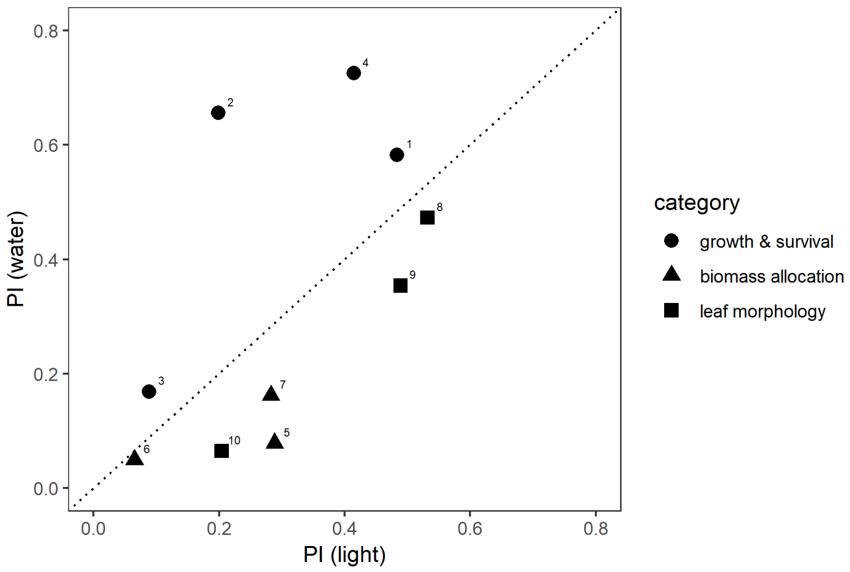


Figure 4.5 Plasticity index of traits among light treatments vs. among water treatments in wiregrass plants. Numbers indicate the variables as listed in Table 2

DISCUSSION

Effects of drought and shade on wiregrass growth

Drought and shade showed independent effects on wiregrass growth. Support for the uncoupled hypothesis on the effect of drought and shade on plants is evidenced by the lack of an interaction found between water and light treatments on wiregrass growth, biomass allocation, and leaf morphology in our experiment. Wiregrass responded to drought and shade independently through changes in functional traits, although one limiting resource (e.g. water) can affect the response to the other limiting resource (e.g. light) (Bloom et al. 1985; Chapin et al. 1987; Valladares et al. 2007) but not in an interactive manner. The lack of an interactive effect of drought and shade on wiregrass may have been because shade levels (down to 20% light) in our experiment were not limiting to wiregrass. This may result in wiregrass being able to maintain its biomass under different levels of light availability but under the same water level, as observed in this study. Our lowest light treatment (20%) was similar to the dark end of the forest habitat of wiregrass, but this level was not as dark as employed by other studies, e.g.

studies listed in the Supplementary Material of Holmgren et al. (2012). This meta-analysis of field and glasshouse studies on the interactive effects of drought and shade indicated that facilitation is likely in moderate shade (Holmgren and Scheffer 2010) while trade-off is likely in deep shade. This suggests switches of effects along the stress gradients (Holmgren et al. 1997; Maestre et al. 2009; Michalet et al. 2006). While our study did not consider the effect of very deep shade (< 20% light) on droughted plants, our results also did not show a facilitative effect of moderate shade on drought plants.

Shade did not weaken the effect of drought on growth in our experiment, contrary to what the facilitation hypothesis predicted (Holmgren et al. 1997). We found no evidence that drought plants under shade performed better than under high light, as growth between drought plants in the lowest light (20%) and highest light levels were not significantly different. Similar results have been reported in studies on herbaceous species (Baruch et al. 2000; Muraoka et al. 1997). However, facilitation was evident in others (Benayas et al. 2002; Noda et al. 2004). Differences in the effect of drought and light on these species may be due to differences in the level of stress among these studies. Greenlee and Callaway (1996) showed that facilitation was more evident in high-stress than in low-stress environments. In our study, it may be that drought stress was not long enough in duration to show facilitation effects.

The response of wiregrass to shade did not lead to greater sensitivity to drought, and vice versa, although wiregrass exhibited morphological trade-offs that were consistent with the trade-off hypothesis. First, wiregrass under drought significantly increased allocation to roots at 20% light and this should lead to more sensitivity to low light according to the trade-off hypothesis (Smith and Huston 1989). However, wiregrass under drought was not negatively affected under low light (no significant effect on growth). This is likely because leaf mass fraction was not affected by drought (Amissah et al. 2015) and root mass fraction was not reduced as much as under the well-watered treatment (i.e. root mass fraction under drought at 20% light was significantly higher than that of well-watered plants). Second, wiregrass under shade (20% light) significantly increased its allocation to leaves with increased total leaf area, leaf area ratio, and specific leaf area. All these increase the ability to capture light under shade (Lambers et al. 2008), and support previous findings on plant acclimation to changing light conditions (Evans and Hughes 1961; Loach 1970; Dias-Filho 2000; Solofondranohatra et al. 2021). While allocation to leaves increased under shade, allocation to roots decreased, which should lead plants under shade to become more sensitive to drought according to the trade-off hypothesis (Smith and Huston 1989). However, the growth of wiregrass under the lowest light were not significantly affected by drought. Other morphological or physiological traits not investigated in this study may have offset the impact of having reduced allocation to roots under drought. These could include partial stomatal closure to reduce transpiration rate and thus water loss (Chapin et al. 1987), and increased production of fine roots (Amissah et al. 2015) or increased length to volume ratio of fine roots (Ryser and Eek 2000) that both increase surface area for water absorption.

The plastic adjustments in biomass allocation and leaf morphology enabled wiregrass to maximize the capture of the limiting resource (light) under the same water level. These phenotypic plastic responses are most likely the mechanisms used by wiregrass to maintain growth under changing light availability (Ryser and Eek 2000; Sultan 2000; Valladares et al. 2007).

Although the response of wiregrass to drought and shade is uncoupled in our experiment as discussed above, this does not necessarily mean that canopy cover and water stress in forest systems are also uncoupled. Evaporation in open areas without tree canopy can be much faster than in shaded areas with tree canopy cover. As such, wiregrass in forested areas with shade are likely to experience lower water stress than those in open areas, despite the same rainfall or drought condition.

The phenotypic plasticity displayed by wiregrass in our study suggests that it can persist under changing conditions brought about by some disturbances (e.g. wildfire, logging) and climate change. However, our results also suggest that, under changing conditions, the abundance of wiregrass in the understorey can be limited by water. Wiregrass growth was more sensitive to changes in water level than light level in our experiment, as shown by greater variations in growth in response to water than light based on the plasticity index (Couso and Fernández 2012).

Implications for forest flammability and climate change

The high biomass load of wiregrass when water is not limiting could strongly influence flammability in the forest understorey. High biomass or abundance of flammable grass is reported as a key driver of flammability (Rossiter et al. 2003; Setterfield et al. 2010), particularly combustibility and sustainability (Simpson et al. 2016). Therefore, periods of increased wiregrass abundance when water is not limiting could become windows of increased flammability due to increased fuel continuity and fuel load of fine leaves and stems (Buckley 1993). An avenue for further research could be towards understanding the effect of fire itself on wiregrass growth, particularly on total regrown biomass (Simpson et al. 2019; Cadiz et al. 2020).

Our results suggest that reduced precipitation under climate change may lead to decreased wiregrass abundance (in terms of cover) via a reduction of wiregrass growth. Precipitation is predicted to decrease in south-eastern Australia (Suppiah et al. 2004; Whetton 2011) under future climate conditions. However, the decrease in precipitation in some areas may not reach the point where moisture becomes limiting to wiregrass (e.g. areas with higher canopy cover will have lower rates of evaporation), and consequently reduced rainfall may not significantly reduce wiregrass cover or biomass. A decrease in precipitation could also have implications for the proportion of dead biomass (Nolan et al. 2020). During periods of extreme drought, the increased dead biomass of wiregrass is likely to provide more easily ignitable materials. This can contribute to increased ignitability of the forest understorey where wiregrass is abundant (Buckley 1993).

Limitations of the study

Although our study provides important insights into wiregrass growth, the relatively short timeframe of the glasshouse experiment (12 weeks) could limit the applicability of the results to understanding population dynamics. For example, caution should be applied when using the results to infer changes in wiregrass populations over time in response to canopy cover and seasonal drought in natural ecosystems. That said, the 12-week duration was long enough for trait plasticity to occur in our glasshouse experiment; hence, we are confident about our conclusions on the plastic response of wiregrass to drought and shade. Growth (tiller growth rate and total live biomass) had greater plasticity in response to water availability, whereas biomass allocation and leaf morphology had greater plasticity in response to varying light. This means that wiregrass growth is more sensitive to changes in water availability than changes in light availability because plastic changes in biomass allocation and morphology ensures maximum capture of limiting light. Our discussion of light and water availability impacts on wiregrass abundance (in terms of cover), and possible consequences on flammability must be interpreted with the understanding that other factors, aside from water and light, could also impact wiregrass cover under field conditions.

CONCLUSION

Drought and shade had independent effects on wiregrass growth, hence cover or abundance, supporting the uncoupled hypothesis. The response of wiregrass is mediated by phenotypic plasticity, ultimately resulting in its persistence under limiting water and light. Growth of wiregrass was primarily sensitive to drought stress, suggesting that very dry conditions under climate change are likely to reduce wiregrass abundance but with increased dead biomass, which is likely to provide more easily ignitable materials. On the other hand, in situations where water is not limiting, increased abundance of wiregrass in terms of increased total biomass would likely become windows of increased flammability of the vegetation community.

5 General Discussion

In this chapter, I outline and discuss new knowledge generated throughout this thesis to better understand the drivers of wiregrass distribution and abundance in its native range. An improved understanding of the dynamics of wiregrass is critical, as this species disproportionately affects forest flammability and has a wide distribution in south-eastern Australia. I summarise the results from Chapters 2-4 that address the specific aims of this thesis which are to investigate (1) how the environmental factors affect the distribution of wiregrass within its range; (2) how the environmental factors influence the abundance of wiregrass within its range; and (3) the effect of resource availability on wiregrass biomass. Then I use these results to address the overarching question: *How does wiregrass become prolific within its range?* The results are also used to address the last aim of this thesis which is to investigate the potential effect of climate change on wiregrass distribution and abundance. Finally, I discuss the significance of the results for forest flammability under current climatic conditions and future climate scenarios. Limitations of this thesis and future research directions are also incorporated into the discussion.

KEY ENVIRONMENTAL FACTORS AFFECTING THE DYNAMICS OF WIREGRASS

Wiregrass has a broad distribution in south-eastern Australia, occupying a range of eucalypt forests. Modelling of wiregrass distribution in this region using MaxEnt (Chapter 2) identified key factors associated with this distribution – temperature, moisture, and soil pH. Wiregrass most frequently occurs in relatively cool sites with less temperature variation, less rainfall variation, average precipitation of the driest month higher than 4 mm, and in very acidic soils (Figure 5.1). These conditions describe areas of suitable habitat for wiregrass. However, it also grows beyond this range. Wiregrass can be highly tolerant of environmental extremes and disturbances (e.g. drought, low light, high intensity fires) and will adjust its morphology rather than completely die (Chapters 3 and 4, Cadiz *et al.* 2020, 2021). As such, it is likely that wiregrass will persist under future climate change, even as areas of highly suitable habitat contract (Chapter 2).

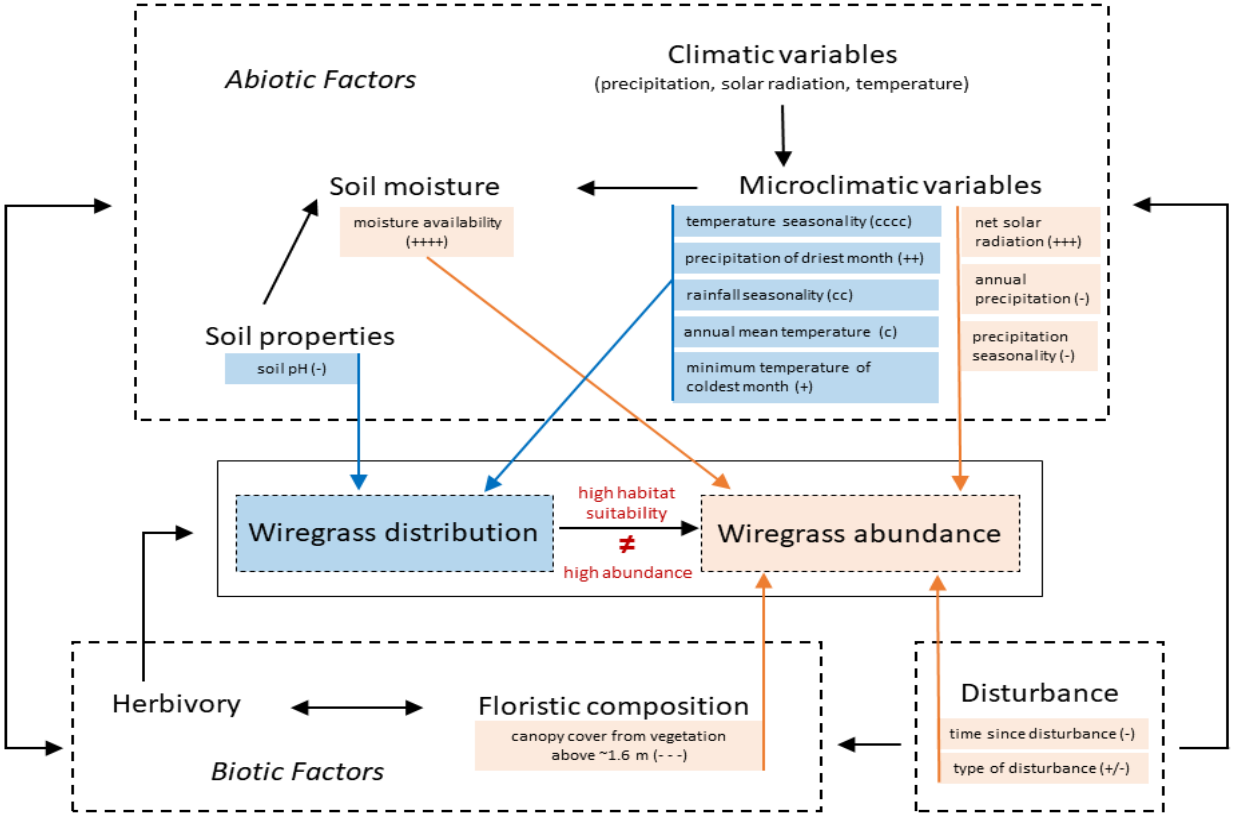


Figure 5.1 Conceptual model of the distribution and abundance of the wiregrass *Tetrarrhena juncea* R. Br. as influenced by environmental factors. This study primarily investigates the influence of *abiotic* environmental factors. The coloured boxes (blue for abundance; orange for distribution) indicate the knowledge generated by this thesis to fill the information gap presented in Chapter 1. Specific factors are indicated in coloured boxes under each category. The positive (+) and negative (-) symbols indicate the approximately linear relationship of the factors to wiregrass distribution/abundance; non-linear relationships are indicated with the ‘c’ symbol. The number of symbols indicate the importance of the factor relative to the other factors associated with distribution/abundance.

Highly suitable habitats do not necessarily harbor abundant wiregrass (Figure 5.2), but where wiregrass is present, there are three conditions that will greatly favour its growth, hence dominance. One important condition is the availability of water, which is a strong predictor of wiregrass biomass (Chapter 4, Cadiz *et al.* 2021). Wiregrass biomass tends to vary positively with water availability (Figure 5.1, Chapter 4, Cadiz *et al.* 2021). This result matches the species distribution modelling, where precipitation was also an important determinant of habitat suitability (Chapter 2), but seemingly contradicts the results in Chapter 3 (Cadiz *et al.* 2020), where wiregrass abundance was higher in the drier sites. The results in Chapter 3 (Cadiz *et al.* 2020) and the field observations of Ashwell (1985) seemed to indicate that 'drier' conditions promote the abundance of wiregrass. However, these studies were undertaken in wet eucalypt forests, where the 'drier' conditions would not necessarily mean that water is limiting to wiregrass because wet eucalypt forests generally received high rainfall (>1000 mm year^{-1}) (Ashton and Attiwill 1994).

Another environmental factor associated with abundant growth of wiregrass is light availability. Wiregrass cover varies positively with increased light availability (Figure 5.1, Chapter 3, Cadiz *et al.* 2020). Net solar radiation and canopy cover were the top predictors of variation in wiregrass abundance in the wet forests of the Central Highlands of Victoria (Chapter 3, Cadiz *et al.* 2020), suggesting that light availability influences the abundance of wiregrass. Ashwell (1985) also suggested light availability explained much of the variation in wiregrass abundance in the wet forest of Sherbrooke Forest Park. However, the results of the experimental manipulation in Chapter 4 (Cadiz *et al.* 2021) strongly suggest light is less important than water availability to wiregrass abundance. The higher importance of water than light (Chapter 4, Cadiz *et al.* 2021) in explaining variation in wiregrass biomass can explain why high abundance of wiregrass is sometimes found in stands with high canopy cover (Chapter 3, Cadiz *et al.* 2020). While wiregrass is observed to abound under canopy gaps (Ashton 2000) or in more illuminated stands (Ashwell 1985), abundant wiregrass (at most 76% cover) is also observed under shaded areas ($\geq$ 90% canopy cover) in Mountain Ash-dominated wet forest (Chapter 3, Cadiz *et al.* 2020).

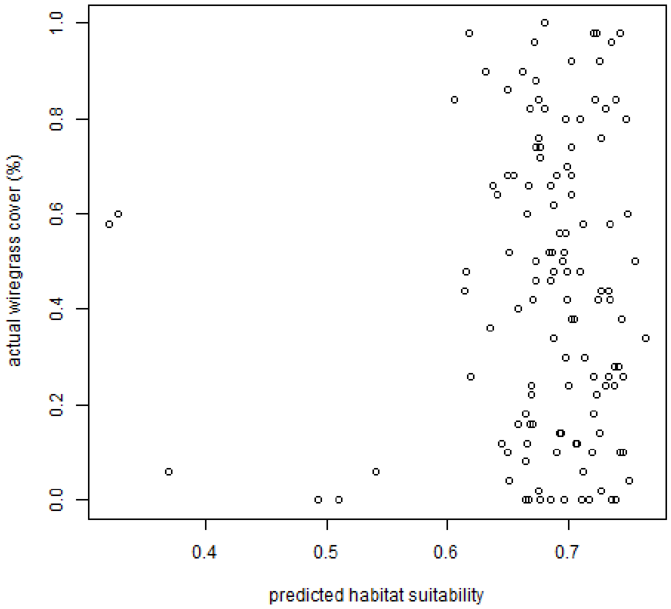


Figure 5.2 Habitat suitability vs. wiregrass cover in the Mountain Ash-dominated forest in the Central Highlands of Victoria. Predicted habitat suitability is derived from the MaxEnt model of species distribution (Chapter 2); wiregrass cover is taken from actual field survey data (Chapter 3, Cadiz *et al.* 2020). Out of 126 sites, 120 are categorized by the MaxEnt model (Chapter 2) as highly suitable (habitat suitability value > 0.6). In these highly suitable sites, wiregrass cover varied greatly. Predicted high habitat suitability does not necessarily correspond to high wiregrass cover or abundance.

Lastly, recent disturbances that do not compromise the reservoir of wiregrass propagules can promote abundant regeneration (Figure 5.1, Chapter 3, Cadiz *et al.* 2020). The field study in Chapter 3 (Cadiz *et al.* 2020) found higher levels of wiregrass post-fire compared with logging, presumably because the propagules were damaged during soil disturbance caused by logging. Recovery of wiregrass occurs rapidly in the initial years post-fire. Fogarty (1993) found that wiregrass can recover most of its average long-term load (16 tons/hectare) in about 15 years after fire, but half that load is reached in about four years. The response curve of wiregrass abundance as a function of time since disturbance, as presented in Chapter 3 (Cadiz *et al.* 2020), did not include the first seven years after fire. As such, it did not capture the initial flush of growth post-fire. Instead, it showed a gradual decline of wiregrass cover over time. A response that included the first seven years post-fire would most likely show increasing wiregrass cover in the years immediately post-fire, a peak in cover before seven years post-fire, and then a gradual decline after that (Chapter 3, Cadiz *et al.* 2020).

Two caveats should be considered when interpreting these results. Firstly, this study focuses primarily on the influence of abiotic environmental factors and does not consider the influence of potentially important biotic factors, such as herbivory and competition. Herbivores like the wombat (*Vombatus ursinus* Shaw, 1800) (Ashwell 1985; Ashton and Chappill 1989), sambar deer (*Cervus unicolor* Kerr, 1972) (Forsyth and Davis 2011), eastern grey kangaroo (*Macropus giganteus* Shaw, 1790) and black wallaby (*Wallabia bicolor* Desmarest, 1804) (de Munk 1999) reportedly graze on wiregrass. The wombat is thought to be the most important wiregrass grazer that could significantly reduce wiregrass cover (Ashwell 1985; Ashton and Chappill 1989). However, quantifying grazing pressures caused by several species across large areas is challenging. On the other hand, plants competing with wiregrass for available resources (e.g. soil moisture, light, space) could also potentially impact wiregrass abundance. For example, the fern *Polystichum proliferum* competes with wiregrass for space, and the tree stratum competes with wiregrass for light; when their covers decrease, wiregrass abundance potentially increases (Ashwell 1985). However, quantifying wiregrass competition with different species across different vegetation communities in large areas is difficult. Secondly, the significant factors associated with wiregrass abundance in the correlative modelling (Chapter 3) are not necessarily causal. As such, caution should be exercised when making inferences from these results. The correlative nature of the method might help explain why the importance of factors sometimes varied between the studies.

HOW DOES WIREGRASS BECOME PROLIFIC WITHIN ITS RANGE?

The results of this study strongly suggest two salient abiotic conditions that cause wiregrass to become prolific within its range – *increased resource availability* and *disturbance*. This is evidenced by the three key findings. First, wiregrass biomass is high when the water resource is non-limiting (Chapter 4, Cadiz *et al.* 2021). This is consistent with the observation that wiregrass is often abundant in Mountain Ash-dominated wet forests where average annual precipitation is high (Ashwell 1985; Cadiz *et al.* 2020). Second, when moisture is non-limiting, wiregrass cover is high in forest stands with reduced canopy cover and increased light (Chapter 3, Cadiz *et al.* 2020). This agrees with the observations of Ashton (2000) and Ashwell (1985) that wiregrass abounds under gaps and illuminated sites in the wet forests. Third, wiregrass cover is high in recently disturbed areas (Chapter 3, Cadiz *et al.* 2020). Wiregrass has the ability to readily exploit recently-burnt areas with vegetative regeneration, and with its seeds being stimulated to germinate by smoke (Penman *et al.* 2008). Wapstra *et al.* (2003) reported that in Tasmania, wiregrass is more pronounced in greatly disturbed areas.

A disturbance is associated with an increase in resource availability (Sher and Hyatt 1999). A fire disturbance in a forest, for example, can decrease the canopy cover, consequently increasing the light reaching the forest floor. Fire can also kill plants, reducing the density of the plant population, consequently decreasing competition. Hence, the light resource is increased in two ways – via reductions in canopy cover and competition. The increase in resource availability associated with disturbance can explain why disturbances are associated with increased abundance of wiregrass.

However, an increase in resource availability is not the only effect that disturbance has on the vegetation community. Disturbances can also provide the stimulus for regeneration of some plant species, which contributes to the abundance or dominance of species (Gill 1981; Penman *et al.* 2008). In the case of wiregrass, the seed is stimulated to germinate by smoke from fires (Penman *et al.* 2008).

Interestingly, the two salient conditions that influence the abundance of native wiregrass as discussed above correspond to two hypotheses explaining the success of exotic invasive species in their invaded community: *increased resource availability hypothesis* (Sher and Hyatt 1999; Hood and Naiman 2000; Colautti *et al.* 2006) and *disturbance hypothesis* (Elton 1958; Hobbs and Huenneke 1992). The increased resource availability hypothesis proposes that the success of an exotic species in invading a new site increases with the availability of resources (Sher and Hyatt 1999;

Hood and Naiman 2000; Colautti *et al.* 2006). According to the disturbance hypothesis, an exotic species has higher success invading a disturbed site than a relatively undisturbed one (Elton 1958; Hobbs and Huenneke 1992). Increased resources and disturbance are the same factors that cause other native species to become unusually dominant within their range. For example, Pivello *et al.* (2018) reported that anthropogenic disturbances (i.e. habitat fragmentation, forest gap formation, wildfires) are the key drivers of the explosive population growth of Brazilian 'super-dominant' native species, which include woody bamboos, lianas, palms, ferns, and some trees. Another example is the dominance of the native fern *Dennstaedtia punctilobula* in Canadian forest understories; this species has become invasive in its own range due to increased light availability in the understorey following overstorey thinning and removal of competitor plant species by herbivory (de la Cretaz and Kelty 1999). It appears that the 'problematic' native species and the exotic invasive species exploit the same opportunities to become dominant; that is, when resources are increased, and the vegetation community is substantially disturbed.

SIGNIFICANCE AND IMPLICATIONS

The potential effect of climate change on wiregrass distribution and abundance

Predicting the effect of climate change on wiregrass distribution and abundance is complex. While some climatic factors are expected to make conditions less favourable for wiregrass, higher wildfire frequencies, caused by climate change, could make conditions more favourable to wiregrass. Another layer of complexity is the uncertainty about how the climate will change. This thesis used three different future climate scenarios to account for that uncertainty – a) hot and dry, b) hot and with the same moisture as the current condition, and c) hot and wet (Suppiah *et al.* 2007; Whetton 2011; Putnam and Broecker 2017). Predictions of the effects of these different conditions on wiregrass distribution and abundance are discussed below based on the results of this study and a broader understanding of the physiology of plants in response to heat stress. The effect of increases in temperatures to plants via heat stress depends on the heat tolerance of the plant species (Taiz and Zeiger 2002; Lambers *et al.*

2008). Heat stress sustained for long periods can negatively impact the growth and development of plants. However, heat stress can be alleviated by moisture availability (Taiz and Zeiger 2002; Lambers *et al.* 2008). The heat tolerance of wiregrass was not determined experimentally in this study, nor how the increases in temperature may interact with moisture availability and canopy cover to impact wiregrass abundance. Future studies that address these knowledge gaps will be beneficial to improve the predictions on how wiregrass distribution and abundance would change under future climate scenarios. While the physiological heat tolerance of wiregrass is unknown, the MaxEnt model for wiregrass distribution gives us some idea on the temperature preference of wiregrass – that it occurs in areas with less temperature variation, with annual mean temperature within 8 to 18 °C, and minimum temperature of coldest month not falling below -4 °C. In other words, wiregrass prefers a relatively stable, cool temperature.

The 'hot-dry' climate scenario has the largest predicted impact on wiregrass, with both distribution and abundance declining for this scenario (Table 5.1). Wiregrass distribution is mainly associated with temperature. Increases in temperature or greater seasonal variations in temperature are predicted to decrease wiregrass distribution. Increased temperature will most probably cause heat stress to wiregrass, and this will be exacerbated by dry conditions. Prolonged heat and water stresses will likely lead to decreased growth, or even death (Taiz and Zeiger 2002; Lambers *et al.* 2008). However, wiregrass will most likely persist, rather than being eliminated entirely. Wiregrass tolerates very dry conditions – it remains alive, albeit at very low abundance (Chapter 4; Ashton and Chappill 1989; Cadiz *et al.* 2021) and can bounce back to its prior vigour after severe drought (Ashton and Chappill 1989). Wiregrass abundance is predicted to be severely affected under dry conditions since moisture availability is a strong driver of wiregrass abundance (Chapter 4, Cadiz *et al.* 2021). Furthermore, increased temperatures will exacerbate soil dryness through evaporation, which could further lead to decreased abundance.

Table 5.1 Predicted effect of different climate scenarios to wiregrass distribution and abundance. (+++/---: effect is high; ++/--: effect is moderate; +/-: effect is low; ns: effect is not significant)

Climate Scenario	Distribution	Abundance
Hot – Dry	- -	- - -
Hot – Same moisture	-	-
Hot – Wet	ns	++

The 'hot-same moisture' climate scenario is predicted to have less effect on wiregrass distribution and abundance than the 'hot-dry' scenario. Heat stress from increased temperatures will likely have a negative impact on wiregrass distribution and abundance but this will be moderated by unchanged moisture availability, so the predicted negative effect is lower than the 'hot-dry' climate scenario.

Under the 'hot-wet' climate scenario, future distribution is predicted to not vary significantly from the current distribution. High moisture availability (wet, non-limiting) could counter the effect of high temperatures, allowing wiregrass to regulate its internal temperature by evapo-transpiration without the threat of reduced moisture and 'dehydration.' The wet condition is predicted to allow wiregrass to significantly increase in abundance even when it is relatively warm.

Forest flammability

Under current climatic conditions, wiregrass dominance exerts a significant influence on the flammability of some forests. Abundant wiregrass either forms thick swards on the forest floor where the mid-storey is under-developed, or thick wall-like 'stooks' extending from the forest floor up to 6 m high where rigid supports are present. With such structural formations, the flammable wiregrass could increase the horizontal and vertical continuity of the fuel bed, hence could increase the spread of fire. Moreover, an abundance of wiregrass increases the fine fuel load of fine leaves and stems (Buckley 1993), hence could increase forest flammability. Wiregrass also makes forests more ignitable – forests with high abundance of wiregrass have a higher moisture threshold for ignition (Buckley 1993). Further research could address questions on the levels of wiregrass abundance that are important to flammability, as well as the relationship between forest structure and wiregrass structure (i.e., sward, 'stooks') that forms a 'three-dimensional' wiregrass cover (horizontal and vertical continuity), and the impact of this structural relationship to forest flammability.

Under future climate scenarios, the potential influence of wiregrass on forest flammability is predicted to decrease where abundance decreases under the 'hot-dry' and 'hot-same moisture' scenarios. However, under a 'hot-wet' scenario where wiregrass is predicted to increase in abundance, it could increase forest flammability and alter fire behaviour in eucalypt forests across south-eastern Australia.

Concluding statement

Overall, I have developed a conceptual understanding of how abiotic environmental factors affect the distribution and abundance of a flammable understorey species, the wiregrass. This led me to identify the conditions under which wiregrass grows prolifically. The high suitability of an area for wiregrass occurrence does not necessarily indicate areas of high wiregrass abundance. Wiregrass grows prolifically when resources (moisture and light) are increased and when the habitat is substantially disturbed. Increases in wiregrass abundance under these conditions could potentially influence forest flammability since wiregrass is a flammable species that could significantly influence fire behaviour. Since the distribution and abundance of wiregrass is primarily influenced by climatic factors, future climate conditions owing to global warming are predicted to alter wiregrass distribution and abundance.

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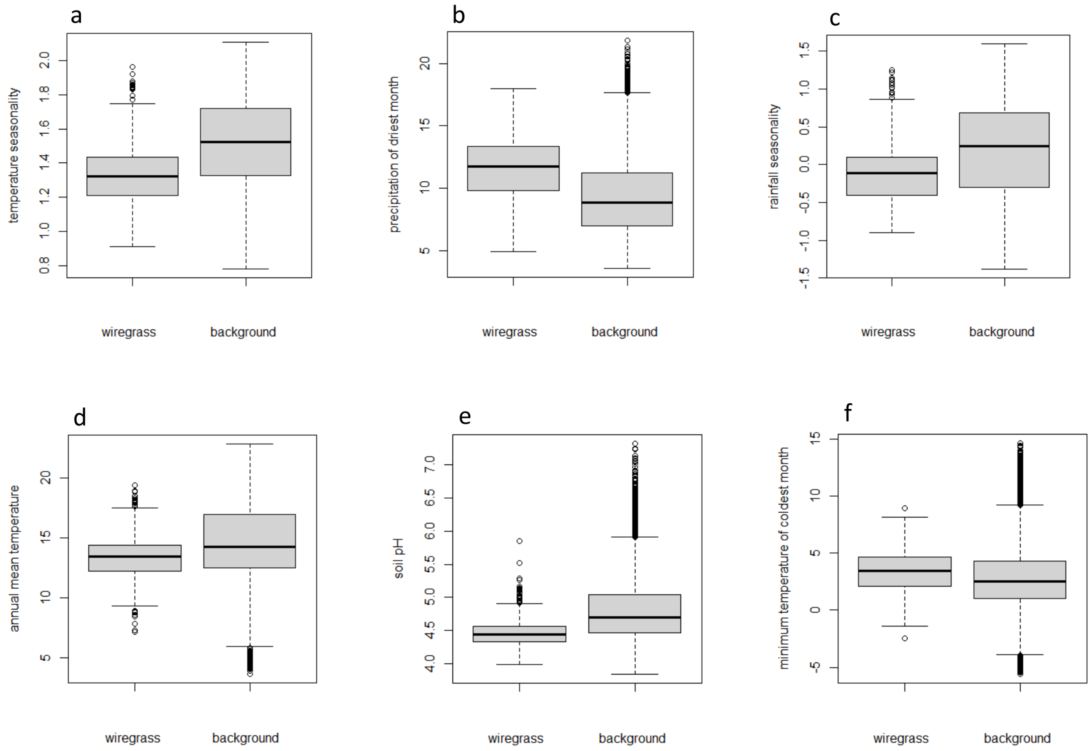
Appendix 1. Chapter 2 supplementary data

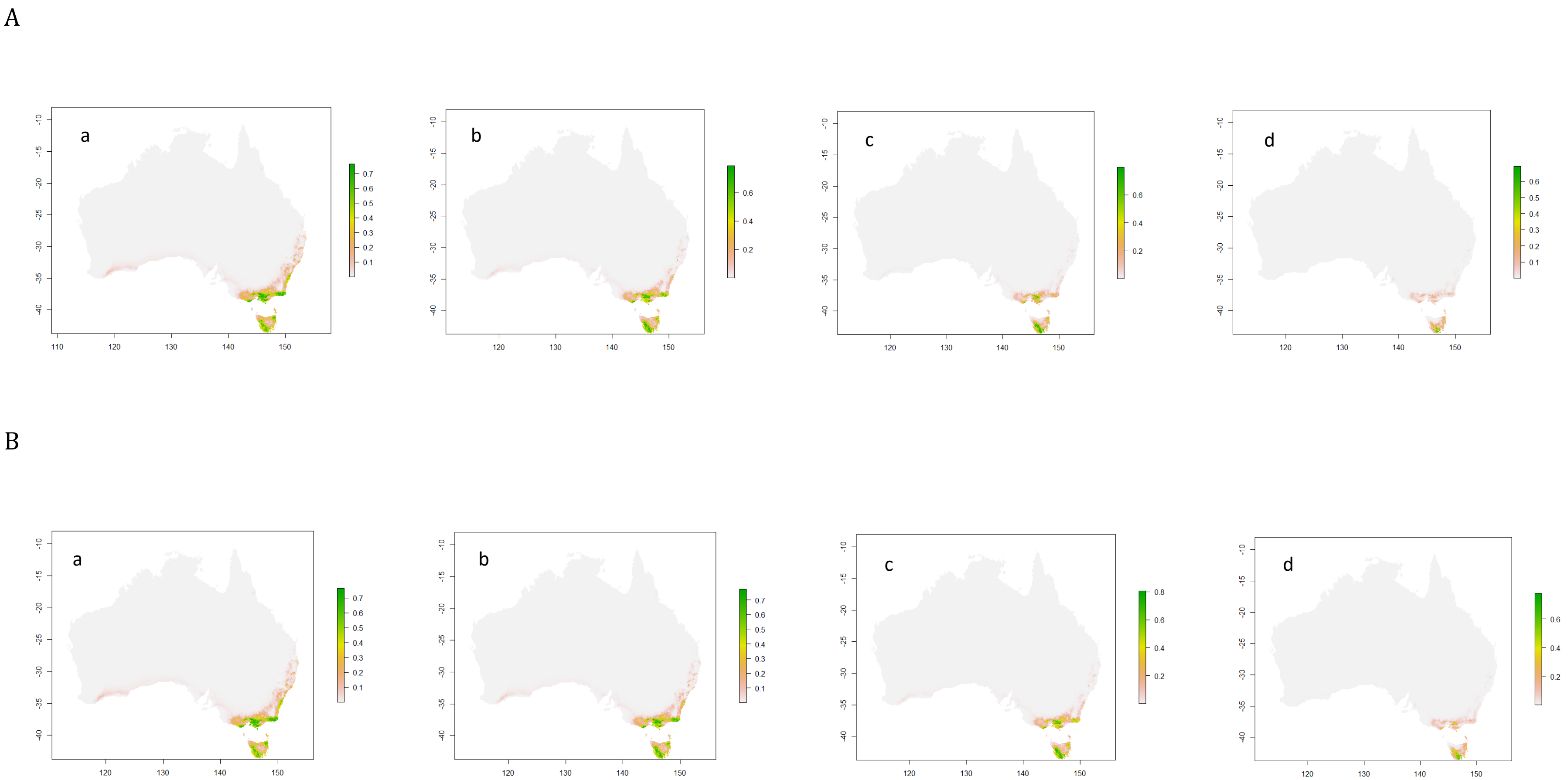
Appendix 1A Pairwise correlations of continuous predictor variables. Correlation values higher than or equal to 0.70 are in **bold.**

Annual mean temperature																					
0.34	Annual mean diurnal range																				
-0.05	**0.76**	Temperature seasonality																			
0.78	**0.77**	0.53	Maximum temperature of warmest month																		
0.76	-0.30	-0.61	0.29	Minimum temperature of coldest month																	
-0.18	-0.54	-0.37	-0.47	0.08	Annual precipitation																
-0.63	-0.49	-0.06	-0.62	-0.37	0.55	Precipitation of driest month															
0.18	0.51	0.56	0.56	-0.10	**-0.79**	-0.34	Highest weekly radiation														
-0.50	**-0.70**	-0.53	**-0.76**	-0.05	**0.80**	0.61	**-0.73**	Annual mean moisture index													
-0.55	-0.63	-0.44	-0.68	-0.08	0.50	0.51	-0.39	**0.86**	Mean moisture index of wettest quarter												
-0.22	-0.46	-0.33	-0.52	-0.05	**0.86**	0.50	**-0.81**	**0.76**	0.38	Mean moisture index of driest quarter											
-0.66	0.02	0.45	-0.39	**-0.79**	0.24	0.47	-0.14	0.25	0.13	0.38	Elevation										
0.49	0.00	-0.18	0.15	0.35	0.58	-0.11	-0.56	0.26	-0.07	0.64	0.01	Summer rainfall									
-0.65	-0.58	-0.19	-0.65	-0.25	0.64	**0.72**	-0.42	0.65	0.60	0.38	0.32	-0.23	Winter rainfall								
0.67	0.44	0.10	0.50	0.26	-0.07	-0.48	-0.08	-0.34	-0.59	0.15	-0.08	**0.73**	**-0.76**	Rainfall seasonality							
-0.32	-0.02	0.10	-0.26	-0.36	0.32	0.29	-0.29	0.35	0.21	0.39	0.44	0.19	0.22	0.04	Ruggedness						
-0.28	-0.03	0.08	-0.23	-0.31	0.28	0.26	-0.25	0.31	0.18	0.34	0.37	0.16	0.19	0.03	**0.88**	Slope					
-0.15	0.11	0.17	-0.04	-0.24	0.01	0.05	-0.08	-0.07	-0.17	0.07	0.22	-0.04	0.09	-0.03	-0.04	-0.06	Available water capacity				
0.57	0.39	0.14	0.63	0.39	-0.69	-0.61	0.60	**-0.75**	-0.53	**-0.71**	-0.58	-0.25	-0.57	0.17	-0.66	-0.58	-0.13	Bulk density			
-0.13	-0.08	-0.01	-0.12	-0.08	0.34	0.15	-0.35	0.15	-0.04	0.29	0.13	0.09	0.37	-0.13	0.08	0.07	0.38	-0.22	Clay		
0.44	0.67	0.45	0.64	0.01	-0.53	-0.55	0.36	**-0.76**	**-0.73**	-0.46	-0.16	-0.03	-0.52	0.37	-0.16	-0.14	0.22	0.49	0.20	Soil pH	
-0.71	-0.58	-0.28	**-0.74**	-0.31	0.56	0.67	-0.49	**0.72**	0.63	0.46	0.38	-0.16	**0.80**	-0.59	0.24	0.21	0.10	-0.62	0.30	-0.58	Organic carbon

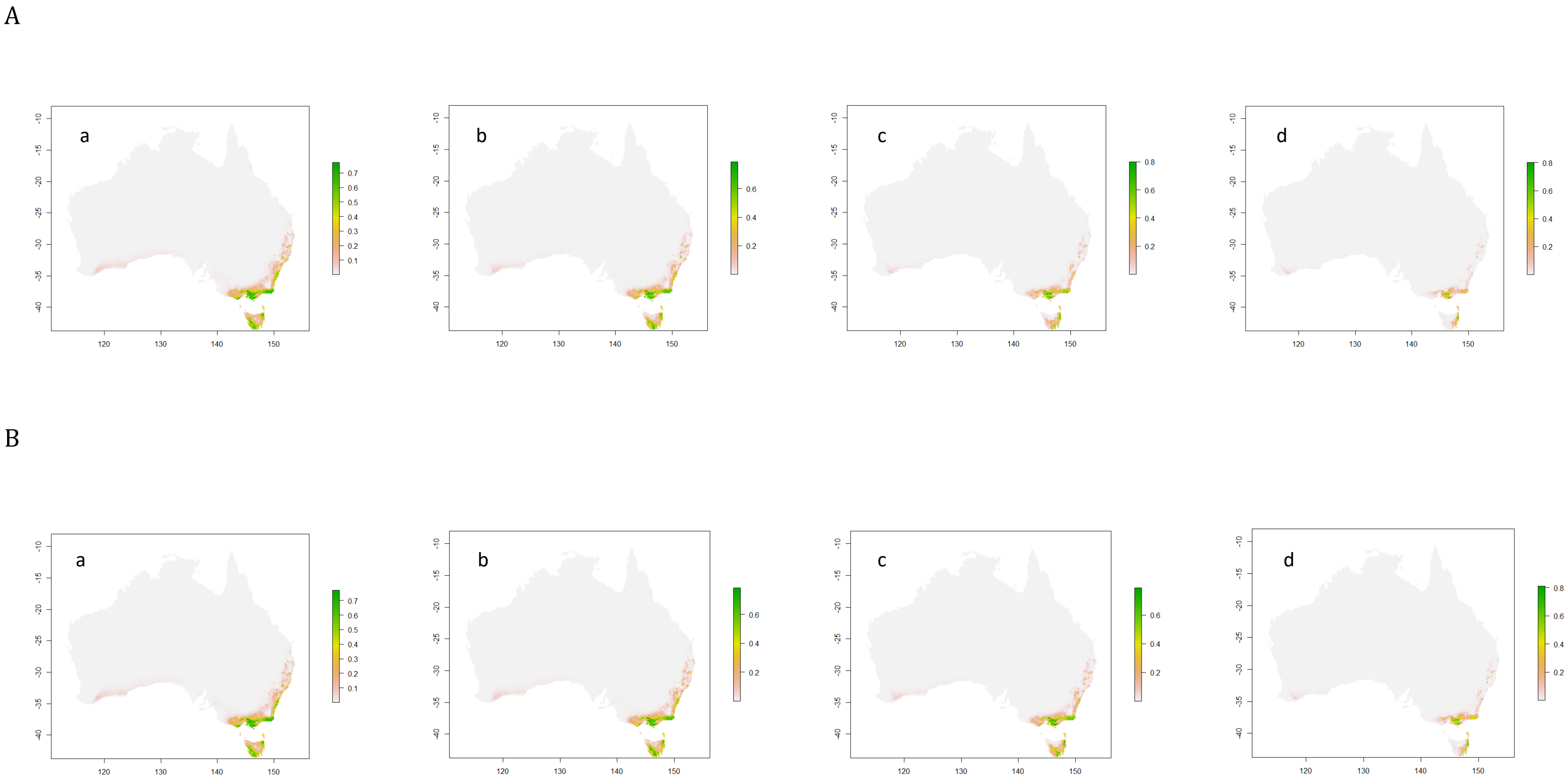
Appendix 1B Comparison of predictor values between the wiregrass and background points: a) temperature seasonality, b) precipitation of driest month, c) rainfall seasonality, d) annual mean temperature, e) soil pH, and f) minimum temperature of coldest month. Mean differences for all variable comparisons were significant (p-value < 0.01).



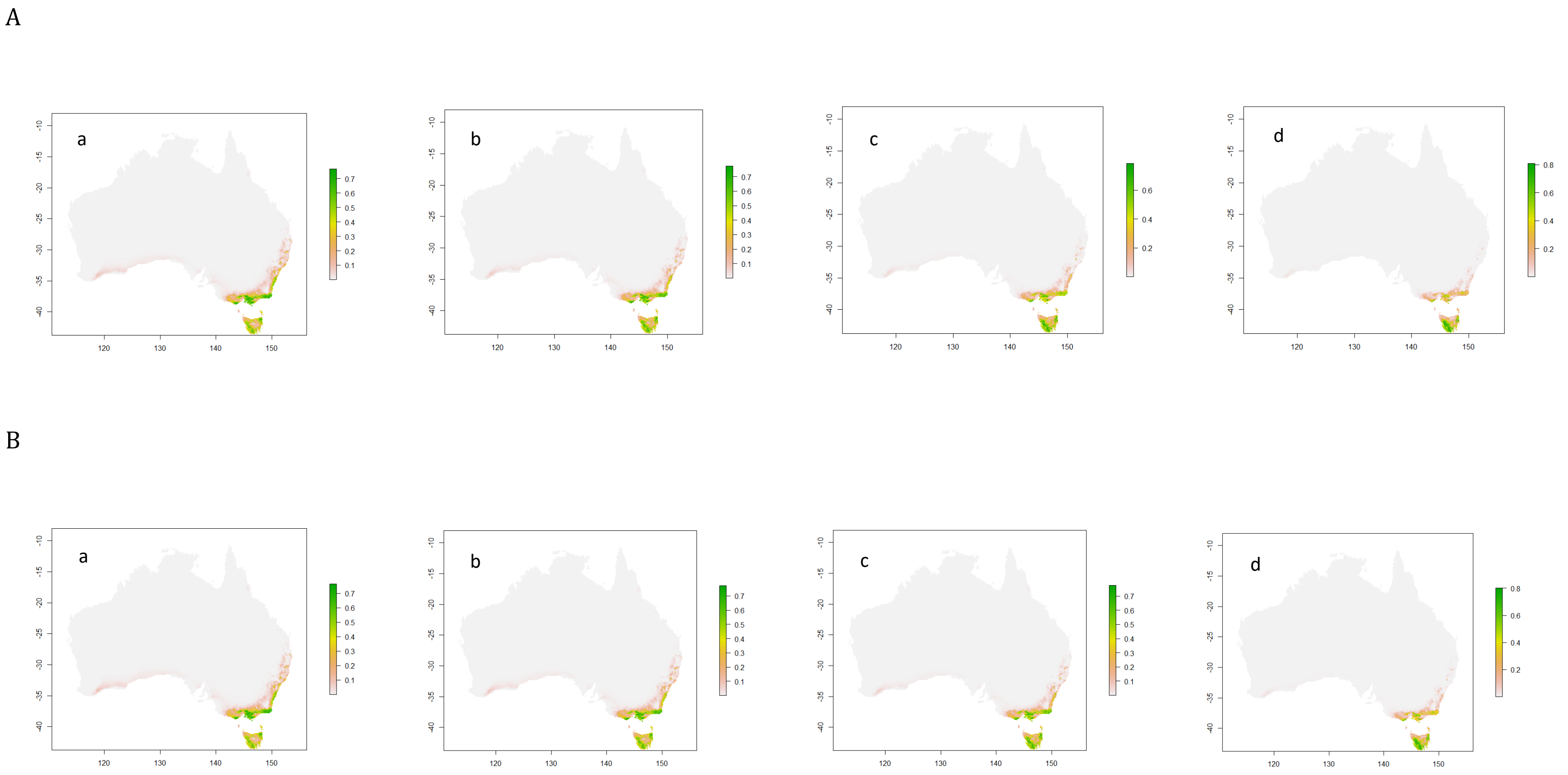
Appendix 1C Future predictions of wiregrass distributions based on climate change projections from four global circulation models (I. CSIRO-Mk3; II. GDFL-CM2; III. MPMP-ECHAM5; IV. UKMOHADCM3), following (A) A1FI high emission scenario, and (B) A2 mid-range emission scenario.



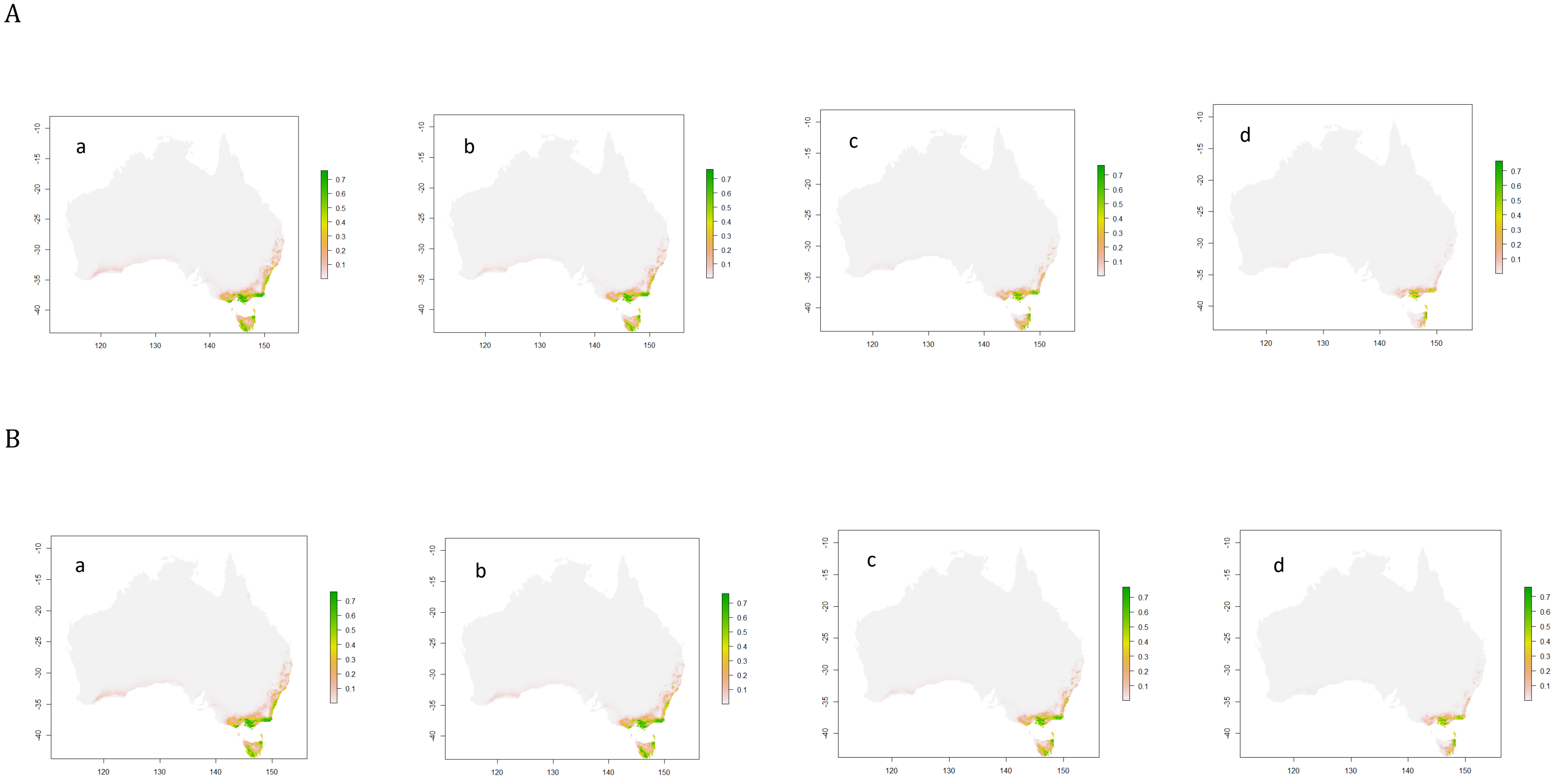
I. Future predictions (a. 2030, b. 2050, c. 20170, d. 2100) of habitat suitability for forest wiregrass *Tetrarrhena juncea* R.Br. according to climate change projections of CSIRO-Mk3, following (A) A1FI high emission scenario, and (B) A2 mid-range emission scenario.



II. Future predictions (a. 2030, b. 2050, c. 20170, d. 2100) of habitat suitability for forest wiregrass *Tetrarrhena juncea* R.Br. according to climate change projections of GDFL-CM2, following (A) A1FI high emission scenario, and (B) A2 mid-range emission scenario.



III. Future predictions (a. 2030, b. 2050, c. 20170, d. 2100) of habitat suitability for forest wiregrass *Tetrarrhena juncea* R.Br. according to climate change projections of MPMP-ECHAM5, following (A) A1FI high emission scenario, and (B) A2 mid-range emission scenario.



IV. Future predictions (a. 2030, b. 2050, c. 20170, d. 2100) of habitat suitability for forest wiregrass *Tetrarrhena juncea* R.Br. according to climate change projections of UKMOHADCM3, following (A) A1FI high emission scenario, and (B) A2 mid-range emission scenario.

Appendix 2. Chapter 3 supplementary data

Pairwise correlations of continuous predictor variables. Correlation values higher than or equal to 0.70 are in **bold**.

canopy cover																							
0.04	aspect																						
0.05	-0.06	elevation																					
-0.03	**-0.79**	0.17	net solar radiation																				
0.35	-0.03	0.18	-0.06	time since disturbance																			
-0.08	0.05	**-0.92**	-0.16	-0.14	annual mean temperature																		
-0.06	0.08	**-0.83**	-0.10	-0.21	**0.85**	annual mean diurnal range																	
0.07	0.12	**-0.81**	-0.12	-0.08	**0.73**	**0.89**	isothermality																
-0.22	-0.16	0.52	0.12	-0.19	-0.34	-0.40	**-0.73**	temperature seasonality															
-0.15	0.02	**-0.82**	-0.13	-0.22	**0.96**	**0.83**	0.60	-0.06	maximum temperature of warmest month														
-0.05	0.07	**-0.90**	-0.19	-0.07	**0.98**	**0.74**	0.67	-0.36	**0.91**	minimum temperature of coldest month													
-0.24	-0.06	-0.45	-0.01	-0.37	0.61	0.69	0.31	0.38	**0.81**	0.49	temperature annual range												
-0.03	0.09	**-0.93**	-0.16	-0.07	**0.96**	**0.85**	**0.81**	-0.50	**0.87**	**0.95**	0.47	mean temperature of wettest quarter											
-0.13	0.02	**-0.84**	-0.14	-0.19	**0.97**	**0.79**	0.59	-0.10	**0.99**	**0.95**	**0.74**	**0.89**	mean temperature of driest quarter										
-0.13	0.02	**-0.84**	-0.14	-0.19	**0.97**	**0.79**	0.59	-0.10	**0.99**	**0.95**	**0.74**	**0.89**	**1.00**	mean temperature of warmest quarter									
-0.04	0.08	**-0.94**	-0.17	-0.10	**0.98**	**0.86**	**0.81**	-0.49	**0.90**	**0.97**	0.50	**0.98**	**0.92**	**0.92**	mean temperature of coldest quarter								
0.08	-0.01	**0.90**	0.12	0.15	**-0.98**	**-0.81**	-0.67	0.27	**-0.95**	**-0.97**	-0.63	**-0.93**	**-0.97**	**-0.97**	**-0.96**	annual precipitation							
-0.02	-0.07	**0.94**	0.15	0.05	**-0.95**	**-0.80**	**-0.80**	0.56	**-0.83**	**-0.95**	-0.39	**-0.96**	**-0.86**	**-0.86**	**-0.98**	**0.94**	precipitation of wettest month						
0.17	0.09	0.63	0.04	0.29	**-0.78**	-0.69	-0.40	-0.15	**-0.88**	**-0.70**	**-0.85**	-0.62	**-0.85**	**-0.85**	-0.69	**0.81**	0.60	precipitation of driest month					
-0.16	-0.16	**0.73**	0.15	-0.13	-0.60	-0.55	**-0.79**	**0.90**	-0.36	-0.64	0.15	**-0.74**	-0.41	-0.41	**-0.72**	0.56	**0.80**	0.04	precipitation seasonality				
0.01	-0.06	**0.93**	0.14	0.07	**-0.97**	**-0.80**	**-0.76**	0.48	**-0.87**	**-0.97**	-0.46	**-0.97**	**-0.90**	**-0.90**	**-0.98**	**0.97**	**0.99**	0.66	**0.74**	precipitation of wettest quarter			
0.23	0.09	0.54	0.04	0.28	**-0.74**	-0.55	-0.21	-0.35	**-0.88**	-0.69	**-0.87**	-0.57	**-0.87**	**-0.87**	-0.62	**0.78**	0.53	**0.94**	-0.06	0.61	precipitation of driest quarter		
0.23	0.09	0.54	0.04	0.28	**-0.74**	-0.55	-0.21	-0.35	**-0.88**	-0.69	**-0.87**	-0.57	**-0.87**	**-0.87**	-0.62	**0.78**	0.53	**0.94**	-0.06	0.61	**1.00**	precipitation of warmest quarter	
-0.01	-0.07	**0.94**	0.14	0.06	**-0.96**	**-0.81**	**-0.79**	0.54	**-0.84**	**-0.95**	-0.41	**-0.97**	**-0.87**	**-0.87**	**-0.98**	**0.95**	**1.00**	0.61	**0.79**	**1.00**	0.56	0.56	precipitation of coldest quarter

Appendix 3. Chapter 4 supplementary data

Appendix 3a Growth assessed in forest wiregrass *Tetrarrhena juncea* R.Br. grown under varying levels of water and light. W = well-watered; D = drought.

Treatment combinations		Tiller growth rate (cm/day)		Total live biomass (g)		Live biomass proportion		Dead biomass proportion	
Water	Light	Mean	SD	Mean	SD	Mean	SD	Mean	SD
W	20%	1.35	0.42	23.9	5.06	0.958	0.02	0.0417	0.02
W	40%	1.00	0.32	29.1	8.32	0.932	0.03	0.0675	0.03
W	60%	0.99	0.45	24.3	5.38	0.946	0.03	0.0544	0.03
W	80%	0.80	0.60	25.2	9.81	0.927	0.03	0.0725	0.03
W	100%	1.15	0.31	29.7	12.68	0.941	0.02	0.0588	0.02
D	20%	0.57	0.28	9.21	2.90	0.811	0.14	0.189	0.14
D	40%	0.42	0.24	7.99	3.72	0.703	0.19	0.297	0.19
D	60%	0.53	0.19	10.0	3.44	0.785	0.12	0.215	0.12
D	80%	0.25	0.14	8.93	2.86	0.788	0.14	0.212	0.14
D	100%	0.46	0.25	8.85	2.17	0.823	0.12	0.177	0.12

Appendix 3b Biomass allocation assessed in forest wiregrass *Tetrarrhena juncea* R.Br. grown under varying levels of water and light. *W* = well-watered; *D* = drought.

Treatment combinations		Leaf mass fraction		Stem mass fraction		Root mass fraction	
Water	Light	Mean	SD	Mean	SD	Mean	SD
W	20%	0.227	0.04	0.666	0.07	0.107	0.04
W	40%	0.181	0.03	0.677	0.08	0.141	0.06
W	60%	0.204	0.04	0.642	0.07	0.154	0.04
W	80%	0.178	0.04	0.661	0.10	0.161	0.07
W	100%	0.187	0.03	0.657	0.08	0.156	0.06
D	20%	0.258	0.05	0.599	0.08	0.142	0.04
D	40%	0.207	0.08	0.612	0.10	0.181	0.05
D	60%	0.195	0.04	0.626	0.07	0.179	0.05
D	80%	0.164	0.06	0.651	0.08	0.185	0.04
D	100%	0.182	0.06	0.649	0.10	0.169	0.05

Appendix 3c Leaf morphology assessed in forest wiregrass *Tetrarrhena juncea* R.Br. grown under varying levels of water and light. *W* = well-watered; *D* = drought.

Treatment combinations		Total leaf area (cm^2)		Leaf area ratio		Specific leaf area (cm^2/g)	
Water	Light	Mean	SD	Mean	SD	Mean	SD
W	20%	47.3	19.80	2.02	0.80	264	33.08
W	40%	28.7	13.48	1.03	0.56	214	14.96
W	60%	26.6	14.65	1.12	0.72	213	20.88
W	80%	21.9	13.46	1.05	0.86	220	26.81
W	100%	27.8	5.38	1.04	0.34	204	18.59
D	20%	22.1	9.82	2.62	1.18	254	27.56
D	40%	17.5	4.27	2.35	0.93	241	28.96
D	60%	14.9	6.73	1.79	1.23	236	39.30
D	80%	10.5	4.26	1.33	0.90	234	29.07
D	100%	14.4	7.65	1.70	0.95	208	30.85

Appendix 3d Average number of days of watering of plants under **drought** treatment.

Block	Light Level	1st watering	2nd watering	# of days between 1st & 2nd watering	3rd watering	# of days between 2nd & 3rd watering	4th watering	# of days between 3rd & 4th watering	5th watering	# of days between 4th & 5th watering	Average # of days per light level
Block 1	20%	2-Apr	13-Apr	11	30-Apr	17	21-May	21			
Block 1	20%	4-Apr	16-Apr	12	30-Apr	14	15-May	15	1-Jun	17	
Block 1	20%	29-Mar	10-Apr	12	20-Apr	24	4-May	14	21-May	17	
Block 1	20%	31-Mar	13-Apr	13	30-Apr	17	15-May	15	1-Jun	17	
Block 1	20%	29-Mar	10-Apr	12	27-Apr	17	17-May	20			
Average				**12.0**		**17.8**		**17.0**		**17.0**	**16.0**
Block 1	40%	31-Mar	16-Apr	16	4-May	18	25-May	21			
Block 1	40%	29-Mar	10-Apr	12	25-Apr	15	12-May	17	1-Jun	20	
Block 1	40%	29-Mar	10-Apr	12	20-Apr	10	4-May	14	21-May	17	
Block 1	40%	2-Apr	23-Apr	21	17-May	24					
Block 1	40%	31-Mar	12-Apr	12	27-Apr	15	15-May	18	4-Jun	20	
Average				**14.6**		**16.4**		**17.5**		**19.0**	**16.9**
Block 1	60%	2-Apr	18-Apr	16	8-May	20	1-Jun	24			
Block 1	60%	29-Mar	10-Apr	12	20-Apr	10	4-May	14			
Block 1	60%	29-Mar	10-Apr	12	23-Apr	13	8-May	15	25-May	17	
Block 1	60%	29-Mar	10-Apr	12	23-Apr	13	8-May	15	25-May	17	
Block 1	60%	29-Mar	10-Apr	12	23-Apr	13	8-May	15	25-May	17	

Average				**12.8**		**13.8**		**16.6**		**17.0**	**15.1**
Block 1	80%	2-Apr	18-Apr	16	4-May	16	25-May	21			
Block 1	80%	29-Mar	10-Apr	12	20-Apr	10	4-May	14	17-May	13	
Block 1	80%	29-Mar	10-Apr	12	25-Apr	15	12-May	17	1-Jun	20	
Block 1	80%	29-Mar	10-Apr	12	20-Apr	10	4-May	14			
Block 1	80%	31-Mar	10-Apr	10	20-Apr	10	4-May	14	17-May	13	
Average				**12.4**		**12.2**		**16.0**		**15.3**	**14.0**
Block 1	100%	29-Mar	10-Apr	12	20-Apr	10	4-May	14			
Block 1	100%	29-Mar	10-Apr	12	27-Apr	17	21-May	24			
Block 1	100%	29-Mar	10-Apr	12	20-Apr	10	4-May	14			
Block 1	100%	2-Apr	13-Apr	11	27-Apr	14	8-May	11			
Block 1	100%	29-Mar	10-Apr	12	23-Apr	13	8-May	15	25-May		
Average				**11.8**		**12.8**		**15.6**			**13.4**
Block 2	20%	2-Apr	16-Apr	14	2-May	16	23-May	21			
Block 2	20%	2-Apr	18-Apr	16	8-May	20	1-Jun	24			
Block 2	20%	29-Mar	10-Apr	12	23-Apr	13	8-May	15	25-May	17	
Block 2	20%	29-Mar	10-Apr	12	23-Apr	13	12-May	19	1-Jun	20	
Block 2	20%	2-Apr	12-Apr	10	25-Apr	13	8-May	13	25-May	17	
Average				**12.8**		**15.0**		**18.4**		**18.0**	**16.1**
Block 2	40%	31-Mar	10-Apr	10	20-Apr	10	4-May	14	17-May	13	
Block 2	40%	2-Apr	16-Apr	14	2-May	16	25-May	23			
Block 2	40%	2-Apr	23-Apr	21	21-May	28					
Block 2	40%	29-Mar	10-Apr	12	23-Apr	13	4-May	11	17-May	13	
Block 2	40%	2-Apr	23-Apr	21	15-May	22	4-Jun	20			
Average				**15.6**		**17.8**		**17.0**		**13.0**	**15.9**

Block 2	60%	29-Mar	10-Apr	12	20-Apr	10	4-May	14	21-May	17	
Block 2	60%	31-Mar	10-Apr	10	23-Apr	13	8-May	15	25-May	17	
Block 2	60%	2-Apr	10-Apr	8	30-Apr	20	21-May	21			
Block 2	60%	29-Mar	10-Apr	12	23-Apr	13	8-May	15	25-May	17	
Block 2	60%	29-Mar	10-Apr	12	23-Apr	13	8-May	15	25-May	17	
Average				**10.8**		**13.8**		**16**		**17**	**14.4**
Block 2	80%	31-Mar	10-Apr	10	20-Apr	10	4-May	14	17-May	13	
Block 2	80%	31-Mar	10-Apr	10	20-Apr	10	4-May	14	21-May	17	
Block 2	80%	31-Mar	11-Apr	11	25-Apr	14	12-May	17	25-May	13	
Block 2	80%	31-Mar	10-Apr	10	20-Apr	10	4-May	14	25-May	21	
Block 2	80%	31-Mar	10-Apr	10	23-Apr	13	8-May	15	25-May	17	
Average				**10.2**		**11.4**		**14.8**		**16.2**	**13.2**
Block 2	100%	29-Mar	10-Apr	12	20-Apr	10	4-May	14	21-May	17	
Block 2	100%	2-Apr	16-Apr	14	30-Apr	14	17-May	17	1-Jun	15	
Block 2	100%	31-Mar	10-Apr	10	23-Apr	13	4-May	11	17-May	13	
Block 2	100%	2-Apr	18-Apr	16	8-May	20	25-May	17			
Block 2	100%	29-Mar	10-Apr	12	23-Apr	13	8-May	15	25-May	17	
Average				**12.8**		**14.0**		**14.8**		**15.5**	**14.3**
Block 3	20%	4-Apr	18-Apr	14	2-May	14	21-May	19	4-Jun	14	
Block 3	20%	2-Apr	12-Apr	10	23-Apr	11	4-May	11	17-May	13	
Block 3	20%	31-Mar	10-Apr	10	20-Apr	10	4-May	14			
Block 3	20%	31-Mar	10-Apr	10	23-Apr	13	8-May	15	28-May	20	
Block 3	20%	2-Apr	20-Apr	18	12-May	22	4-Jun	23			
Average				**12.4**		**14.0**		**16.4**		**15.7**	**14.6**
Block 3	40%	29-Mar	10-Apr	12	20-Apr	10	4-May	14	21-May	17	

Block 3	40%	4-Apr	23-Apr	19	12-May	19	4-Jun	23			
Block 3	40%	2-Apr	23-Apr	21	17-May	24					
Block 3	40%	29-Mar	10-Apr	12	23-Apr	13	8-May	15	21-May	13	
Block 3	40%	29-Mar	10-Apr	12	23-Apr	13	12-May	19	1-Jun	20	
Average				**15.2**		**15.8**		**17.8**		**16.7**	**16.4**
Block 3	60%	31-Mar	12-Apr	12	27-Apr	15	12-May	15	1-Jun	20	
Block 3	60%		10-Apr		23-Apr	13	8-May	15	28-May	20	
Block 3	60%	31-Mar	16-Apr	16	4-May	18	25-May	21			
Block 3	60%	2-Apr	18-Apr	16	8-May	20	1-Jun	24			
Block 3	60%	2-Apr	12-Apr	10	27-Apr	15	12-May	15	1-Jun	20	
Average				**13.5**		**16.2**		**18.0**		**20.0**	**16.9**
Block 3	80%	31-Mar	10-Apr	10	23-Apr	13	8-May	15	28-May	20	
Block 3	80%	31-Mar	12-Apr	12	30-Apr	18	21-May	21			
Block 3	80%	29-Mar	10-Apr	12	20-Apr	10	4-May	14	21-May	17	
Block 3	80%	29-Mar	10-Apr	12	23-Apr	13	12-May	19	1-Jun	20	
Block 3	80%	31-Mar	11-Apr	11	27-Apr	16	15-May	18	1-Jun	17	
Average				**11.4**		**14**		**17.4**		**18**	**15.2**
Block 3	100%	29-Mar	10-Apr	12	20-Apr	10	4-May	14			
Block 3	100%	31-Mar	11-Apr	11	25-Apr	14	12-May	17			
Block 3	100%	29-Mar	10-Apr	12	23-Apr	13	8-May	15	25-May	17	
Block 3	100%	31-Mar	10-Apr	10	20-Apr	10	4-May	14	21-May	17	
Block 3	100%	29-Mar	10-Apr	12	23-Apr	13	8-May	15	21-May	13	
Average				**11.4**		**12.0**		**15.0**		**15.7**	**13.5**
									General Average # of Days		**15**