SEEDS, SOILS AND MOISTURE: ECOPHYSIOLOGY TO INFORM MINE SITE RESTORATION IN ARID ZONES

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Submitted in total fulfilment of the requirements for the degree of

Doctor of Philosophy

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November 2019

Conserving biodiversity and reversing the trend of land degradation relies not on our love for nature, but on resolving our disconnect with nature. We must work towards building knowledge and respect for the biophysical restrictions of organisms and ecosystems if we hope to overcome the ecological and cultural consequences of global change.

FORMAT OF THE THESIS

This thesis has been written as a series of stand-alone scientific manuscripts which means that there is some unavoidable duplication of introductory material. Chapter 1 is a general introduction which reviews relevant literature and provides the context and broad aims of the thesis. Chapter 6 is a synthesis and general discussion of the research and its implications. I have formatted the thesis throughout according to a common journal style, hence published chapters were reformatted and figures/tables were renumbered to conform to thesis style.

Some of the work from this thesis has been published or submitted for publication in the following journals:

Chapter 2. Duncan, C., Schultz, N., Lewandrowski, W., Good, M. and Cook, S. (2019) Lower dormancy with rapid germination is an important strategy for seeds in an arid zone with unpredictable rainfall. *PLOS ONE*, 14 (9). DOI: 10.1371/journal.pone.0218421

Chapter 3. Duncan, C., Schultz, N., Good, M., Lewandrowski, W. and Cook, S. (2019) The risk-takers and avoiders: germination sensitivity to water stress in an arid zone with unpredictable rainfall. *AoB PLANTS*, plz066. DOI: 10.1093/aobpla/plz066

Chapter 4. Duncan, C., Good, M., Schultz, N., Sluiter, I. and Cook, S. (2019: submitted) Soil reconstruction after mining fails to reinstate properties crucial for vegetation recovery in arid Australia. *Restoration Ecology*.

DECLARATION

This thesis is the original work of the author, except where explicit acknowledgement to co-authorship of published papers (chapters two, three and four) is provided. For all co-authored papers, I certify that my contribution included the design and implementation of methods, the collection and analysis of all data, and the drafting of manuscripts for submission to journals. The substance of this thesis has not already been submitted for any degree and is not currently being submitted for any other degree or qualification. The thesis is less than 100,000 words in length.

Corrine Duncan

23rd October 2019

SUMMARY / ABSTRACT

Mining in arid regions of Australia is followed by restoration and rehabilitation efforts. However, attempts to reintroduce many woody plant species have been unsuccessful. Water is the key limiting resource to plant growth and seed germination in arid zones. In this thesis, I investigated ecophysiological processes that may help improve recruitment across novel arid landscapes. I tested seed traits and dormancy cues of eight keystone plants and found that six of them had non-dormant, rapidly germinating seeds; a trait we propose is an adaptation to the region's unpredictable rainfall. To identify the germination niche of species, I incubated seeds under different temperatures and water potentials, and found drought avoidance to be an important survival strategy for arid species. I collected soil samples to compare biophysicochemical properties of reconstructed soils to remnant ecosystems, and found that the distribution of clay content in the reconstructed soils did not mirror the remnant soils, compromising their ability to sustain perennial vegetation. I also monitored soil moisture and found that soil reconstruction reduces rainfall infiltration and retention, and subsequently increases evaporation. The synthesis of these results demonstrate some of the limitations to successful restoration in these systems, such as (1) unknown dormancy cues and poor seed longevity, (2) infrequent and episodic plant recruitment due to water limitation, and (3) reduced hydrological function of reconstructed soils. The failure to reinstate hydrological function is the major constraint to ecological restoration in this arid zone. Nonetheless, results from this study suggest that restoration is possible through more strategic use of seed, careful selection of drought tolerant species, and increasing soil moisture. Further failures to reinstate ecosystem function and community dynamics in arid zones with reconstructed soils can be prevented by understanding the edaphic constraints to plant establishment, and ameliorating conditions to mimic ecohydrological processes in remnant ecosystems.

ACKNOWLEDGEMENTS

This project was funded by Tronox Mining, and supported by an Australian Government Research Training Program (RTP) Fee-Offset Scholarship through Federation University Australia. This research would not have been possible without the support and guidance from my supervisors Dr Nick Schultz, Dr Simon Cook, Dr Megan Good and Dr Ian Sluiter. I am eternally grateful for your constructive criticism, encouragement and enthusiasm for my project, particularly to my primary supervisor, Nick Schultz. It has been a privilege to work amongst a team dedicated to the pursuit of quality and innovative approaches to ecological research.

Thank you to Kings Park for trainings in seed based technologies, and importantly, to Wolfgang Lewandrowski. You were my mentor in forming my initial project ideas and overall research goals. I deeply respect your commitment to research, and passion for arid restoration, and look forward to future projects together.

To the Environmental Management Team at Tronox: Thank you for supporting this project financially and for your openness in sharing your approaches to restoration. Your genuine desire for successful restoration outcomes was somewhat unexpected and inspiring. Thank you to Brendan Isaacs (who provided the front cover image) and Sam Summers for access to site, safety inductions and technical support. To the crew from Cully's Earthmoving and Chisholm Earthmoving, thank you for sharing your insights to soil restoration and for installing soil pits. The challenging field component of installing soil moisture probes would not have been possible without the help from Markus Ridgwell. Through sweat, expletives and beers, anything is possible! I'd especially like to thank Tim Zwiersen for your endless enthusiasm for this project and for sharing your knowledge of seed-based technologies to restoration. There are few

projects more challenging than restoring an arid ecosystem during one of the worst droughts in history, and it takes a team of resilient and committed practitioners to achieve Tronox's restoration outcomes.

Finally, I wish to acknowledge the traditional landowners of the region, the past and present Barkindji and Barindji groups, for caring for this country and maintaining these alluring, diverse and sacred arid zones, over tens of thousands of years.

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CHAPTER 1

General introduction and thesis outline

1.1 ARID ECOSYSTEMS

Arid and semi-arid ecosystems cover more than 40% of the global land surface (Reynolds et al. 2007) and over a third of the world's population rely on dry regions for agriculture and resource mining (Millennium Ecosystem Assessment 2005). Dry regions drive interannual variability in global terrestrial CO^2 sinks (Ahlström et al. 2015; Poulter et al. 2014) and, in Australia, arid and semi-arid lands make up 70 per cent, or approximately 5.3 million square hectares, of mainland Australia (Wells 2013). Dry regions are classified by the amount of annual rainfall (Thomas 2011): hyper-arid (< 25 mm), arid (25 - 250 mm) and semi-arid (250 – 500 mm), although these boundaries are set rather arbitrarily because precipitation alone is insufficient for defining climatic boundaries (Huang et al. 2016a; Safriel et al. 2019). For example, some dry regions in northwest Australia are considered semi-arid (Mabbutt 1979), despite a mean annual rainfall greater than 500 mm. Nevertheless, dry regions similarly have high temperatures, highly variable rainfall and frequent droughts, which impose fundamental limits on animal and plant populations (Maestre et al. 2016; Whitford 2002).

For the last 65 years at least, semi-arid regions have been progressively expanding across the globe, either due to arid regions becoming wetter or semi-arid regions encroaching upon humid regions in which the climate has become drier (Cai et al. 2012; Huang et al. 2016a). The current trend towards desertification will likely persist for much longer (Mirzabaev et al. 2019).

Combating desertification and mitigating the effects of drought is one of the most pressing issues today and is a high priority for transitioning to a more sustainable society (UNCCD 1994; UNCCD 2014). Despite these increasing pressures, and the economic, environmental and cultural significance of arid zones, they remain amongst the least-studied of ecosystems, potentially due to their low productivity and remoteness.

Arid ecosystems are sensitive to human activities (Moreno-de las Heras et al. 2018; Xue 1996), and are predicted to exhibit some of the strongest responses to changes in land-use and climate (IPCC 2001; Smith et al. 2000). Climate models predict increasing fluctuations in temperature and timing of precipitation events across the globe (Meehl et al. 2000), with an overall increase in temperatures and greater unpredictability of rainfall in arid zones (IPCC 2012). Global warming will have dramatic effects on semi-arid regions (Huang et al. 2012a; Ji et al. 2014); droughts are expected to become longer and more severe because of enhanced evaporation and reduced precipitation (Dai 2012). Predicted increases in evaporation under climate change will affect soil-moisture balances across the globe, and greater moisture stress is expected for Australia than any other continent (Lioubimtseva 2004). Over the next few decades, average run-off and water availability in some dry regions is projected to decrease by up to 30% (UNCCD 2014) and, as anthropogenic and climate-induced desertification increases across the globe (Safriel et al. 2019), a loss of productive land and a decline in arid ecosystem function is expected (Noojipady et al. 2015; Yang et al. 2010).

1.2 RAINFALL AND COMMUNITY DYNAMICS IN ARID ECOSYSTEMS

Water is the primary resource limiting plant recruitment and growth in arid zones (Chesson et al. 2004; Schwinning and Sala 2004). The timing, intensity, and magnitude of rainfall is highly variable and high solar radiation and temperatures can reduce the biological impact of rainfall events (Noy-Meir 1973; Whitford 2002). The pulse-reserve paradigm describes the way in which such precipitation events trigger pulses of biological production and reproduction that continue until moisture is depleted from the environment (Noy-Meir 1973; Reynolds et al. 2004). The paradigm describes the responses of different functional groups of plants (i.e., shallow rooting grasses or deeper rooting shrub species) to rainfall events (Schwinning and Sala 2004). Small rainfall events of < 5 mm are utilised by microorganisms and lichens (Baldauf et al. 2018; Belnap et al. 2004), but are potentially too small to stimulate growth of short-lived vascular plants, while larger pulses are required for growth and reproduction of tree and shrub species (Fig 1.1). Once water is exhausted from the system, species enter a steady state or ‘zero state’ of no growth or rapid decline (Reynolds et al. 2004), hence wet periods spanning several years may be required to trigger the reorganisation of entire arid communities (Schwinning and Sala 2004).

Our understanding of the effects of rainfall in arid ecosystems has progressed significantly in recent decades, but the relationship between rainfall events and productivity in arid zones is not as simple, nor direct, as initially presumed (Reynolds et al. 2004). Rainfall events in arid zones drive vegetation structure though complex dynamics, which make it difficult to generalise plant and ecosystem responses, and we still do not fully understand the interplay between pulse events and recruitment in arid zones (Reynolds et al. 2004; Wiegand et al. 2004).

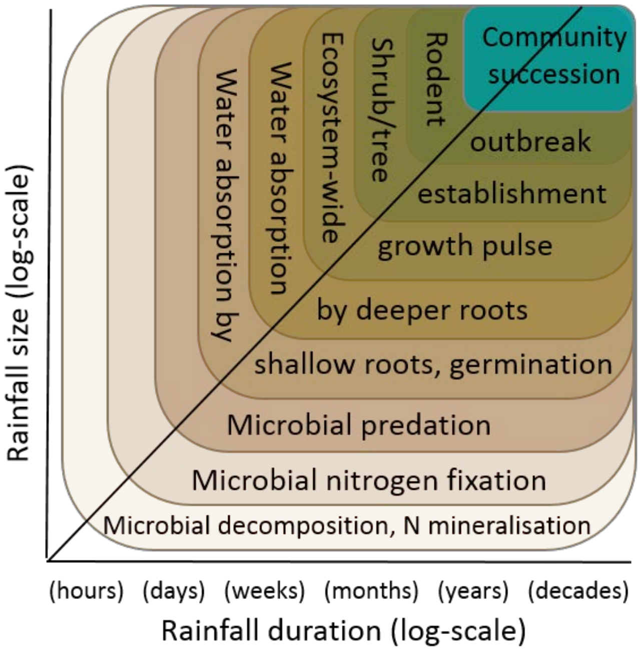

Fig 1.1: The ecological response hierarchy to soil moisture pulses of variable size and duration, developed by Schwinning and Sala (2004). A linear relationship between rainfall size and duration on a log scale is indicated by the solid line. Small and brief rainfall events activate only the physiological rates of soil microbes, whereas larger and longer rainfall events are required to trigger the physiological responses of larger organisms and plants.

Community dynamics in arid zones are related to rainfall patterns because all species have physiological responses to water availability and temperature, that vary across different plant life stages (Bykova et al. 2019; Dürr et al. 2015). If the amount of rainfall falls below thresholds of tolerance for survival and reproduction, necessary biological processes may not occur (Carnicer et al. 2011). What constitutes a biologically meaningful rainfall event depends not only on the response thresholds of species, but also on a complex range of ecological factors including soil properties (Simmers 2003), temperature, microbial activity (Chamizo et al. 2016) and competition from other species (Shiponeni et al. 2011), making it difficult to generalise responses. Plants with shorter life-cycles will likely respond more rapidly to changes in soil moisture content than species with longer life-cycles, including tree species, hence there exists a relationship between the magnitude of rainfall events, the magnitude of ecological responses triggered and the time scale on which these response thresholds unfold (Schwinning and Sala 2004). When rainfall models and species response thresholds are empirically tested and quantified, there is potential to predict community structure under climate change and specific management techniques (Flores et al. 2017; James et al. 2013; Yi et al. 2019). However, the physiological thresholds of native arid species are rarely quantified (e.g.; Arnold et al. 2014b; Hu et al. 2015; Lewandrowski et al. 2018), despite their importance in prescribing community dynamics in arid zones (Gutterman 1993; Reynolds et al. 2004).

1.3 ECOHYDROLOGICAL PROCESSES IN ARID ZONES

Arid zones undergo periods of chronic water shortage, hence do not sustain a continuous cover of plants like mesic regions do (Whitford 2002). Instead, vegetation patterns in arid zones are arranged in mosaic patches of high plant cover and inter-patches with low plant cover (Sala and Aguiar 1996). Vegetation patches and inter-patches are critical for water distribution and infiltration in arid zones, as they serve as basins that capture rainfall runoff, sediments and nutrients (Good et al. 2013; Greene et al. 2001; Muñoz-Robles et al. 2011). Over time these mosaic, and sometimes shifting, distributions of vegetation cause high variability in soil properties across small spatial and temporal scales, due to complex plant–soil feedback responses (Butterfield and Briggs 2009; Qu et al. 2018). These feedback mechanisms significantly impact water fluxes (Quevedo and Francés 2008; Rodriguez-Iturbe 2000) and can reduce ecosystem sensitivity to climate extremes (Ludwig and Tongway 1995). Due to this, deviations from the natural mosaic of vegetation patterns are considered as a degradation of arid ecosystem function (Ludwig 1987).

Soil properties influence the resources available to plants, hence, they also effect the survival and recruitment strategies available to plants (Maestre et al. 2003). Soil physical properties, such as compaction, bulk density and horizon thickness, are important determinants of available water because they effect infiltration and storage rates (Simmers 2003). According to the inverse texture hypothesis, arid zones have higher productivity in coarse soils than fine soils, due to reduced evaporative water loss in the former (Noy-Meir 1973; Sala et al. 1988). Coarser soils may increase plant productivity in species that are adapted, or mature enough, to access moisture from subsoils or from the groundwater. However, fast draining soils may not favour growth at earlier life stages, particularly at the establishment stage, where species are most sensitive to changes in water availability (Chambers 2000; James et al. 2011). The interplay between rainfall events, soil properties and plant recruitment in natural arid ecosystems is not well understood and requires further investigation.

1.4 SURVIVAL STRATEGIES OF ARID-ZONE PLANTS

Germination is extremely sensitive to changes in soil moisture and temperature, and generally germination decreases progressively with decreasing soil water potential (Bradford 1990). In arid species, higher temperatures may not limit germination directly, but will reduce the number of germination events by reducing the temporal window of suitable available soil water (Stevens et al. 2014). Many arid plants are highly adapted to germinate under water stress (Briedé and McKell 1992; Evans and Etherington 1990; Schütz et al. 2002), and tend to have faster germination rates than those from wetter habitats (Jurado and Westoby 1992). Rapid germination and radicle extension are crucial drought survival mechanisms because they ensure establishment before the surface layers of the soil dry out (Bochet et al. 2007; Choinski and Tuohy 1991; Johnson et al. 1996; Stevens et al. 2014). Seed responses at different hydration levels can vary widely, from germination to deterioration and death, whilst some seeds can remain dormant and viable in the soil for many years while fully hydrated (Hegarty 1978). To predict vegetation responses to climate and land-use change, we need to understand the seed physiology that governs plant regeneration in the arid zone (Schwinning et al. 2004).

Arid seeds have evolved to survive extreme climate conditions, and tend to exhibit traits enabling them endure, or avoid, drought conditions (Merino-Martín et al. 2017; Ramírez-Tobías et al. 2014). More than 85% of plant species that grow in arid environments produce seeds that are considered dormant (Baskin and Baskin 2003). Many arid seeds have physiological dormancy, and require a period of temperature stratification, or after-ripening, to relieve dormancy (Baskin and Baskin 2014). Dormancy enables seeds to withhold germination in climatic conditions that are otherwise appropriate for germination of a non-dormant seed (Finch-Savage and Leubner-Metzger 2006). Some dormant seeds can spread germination across multiple seasons, with a proportion remaining dormant and un-germinated, and can be viewed as an example of bet-hedging (Gremer and Venable 2014; Simons 2009). A bet-hedging strategy enables seeds to spread the risk associated with germination across several years, thus sacrificing the potential for short-term reproductive success for enhanced germination through time, and is common in seeds from arid ecosystems (Fan et al. 2018b; Gremer et al. 2016; Lewandrowski et al. 2018). Seeds that rely on lengthy dormancy and bet-hedging strategies to delay, or stagger, germination across multiples seasons, typically also have orthodox seeds; seeds that can survive drying and freezing during ex-situ conservation (Roberts and King 1980). While dormancy is advantageous in natural ecosystems, it may disadvantage some species in the context of restoration and climate change.

1.5 ECOSYSTEM RESTORATION IN ARID ZONES

Ecological restoration is defined as the process of assisting the recovery of an ecosystem that has been degraded or destroyed, back to a degree that the system becomes functional and resilient to periodic stress events (SER 2004). Ecosystem rehabilitation is similar, although the two activities differ in their goals and strategies; rehabilitation emphasizes the reparation of ecosystem processes, productivity and services, whereas the goals of restoration also include re-establishing the community structure and species' composition of the pre-existing ecosystem (SER 2004). Restoration and rehabilitation can be viewed as an attempt to force and accelerate successional processes towards a desired state (Hobbs and Norton 1996), however natural ecosystems typically undergo rapid transitions between states and succession does not always follow an ordered and gradual development (Hobbs 1994; Westoby et al. 1989). For example, woodlands or shrublands that have been invaded by grass species are difficult to restore and the degraded ecosystem may cross a threshold whereby colossal management contributions are required for restoration to a desired state (Aronson et al. 1993). Arid ecosystems undergo high fluxes of resources and productivity in response to climate, hence plant succession is often transient and unpredictable (Miller et al. 2019). To date, attempts to restore the full suite of species that inhabit arid regions prior to disturbance have been unsuccessful (e.g., Cortina et al. 2011; Houerou 2000; Vallejo et al. 2012). The degradation of arid ecosystems effects nearly one billion people, and the productivity of millions of acres of lands are lost every year to desertification, due to a lack of knowledge of how to improve restoration outcomes in arid zones (Bainbridge 2007).

Restoration is generally more costly and difficult in arid and semi-arid ecosystems than in temperate to tropical regions (Fuentes-Castillo et al. 2012; Houerou 2000; Schirmer and Field 2000), because climate is extremely variable and plants exhibit reduced growth rates when water is limited. Slow growth rates of keystone species in response to water deficit impacts the timescales of restoration projects in arid zones (Vicente-Serrano et al. 2013). To complicate the restoration process further, arid plant species often have erratic seeding and flowering events, with highly variable seed production and quality between years (Standish et al. 2007; Wijdeven and Kuzee 2000), and many species rely on co-occurring rainfall events for recruitment (Miller et al. 2019). Erratic plant reproduction in response to unpredictable rainfall events, high temperatures, and nutrient poor soils (Mendez and Maier 2008; Peters 2000; Sheoran et al. 2010) can severely impede restoration outcomes in arid zones (James et al. 2011; Madsen et al. 2016).

Acquiring the amount of seed required for large-scale restoration projects is challenging, and most of the world's seed banks dedicated to native species have seed holdings that are barely sufficient to provide seed for but a few percent of the areas in need (Merritt and Dixon 2011). Seeds used for restoration are typically stored in unnatural conditions, often for years, and it is unclear how storage conditions impact seed viability in most uncultivated arid species (Crawford 2013). Furthermore, without knowledge of seed dormancy traits, seeds used in restoration projects may be stored in conditions causing dormancy loss and, consequentially, triggering germination and increasing the probably of seed death or growth outside of the plant's environmental niche (Ensslin et al. 2018). Less than 10% of seeds used for arid restoration result in establishment (James et al. 2011; Merritt and Dixon 2011; Williams et al. 2002) and meeting the demand for seed required for restoration will rely on better understanding dormancy cues and the germination niche of species (Rokich and Dixon 2007; Wijdeven and Kuzee 2000). Improving the notoriously low success rates of arid zone restoration is increasingly urgent at a global scale, given the large number of mining and agricultural operations located within arid and semi-arid regions across the globe (Gratzfeld 2003).

1.6 ARID ECOSYSTEM RESTORATION AFTER MINING

Mining for deep mineral resources presents the most severe form of anthropogenic disturbance, due to the volume of material moved (Lin et al. 2005). Consequently, reinstating vegetation is slower and more challenging following mining than other disturbances, such as land clearing and fire (Fox et al. 1996). Where mining operations remove or totally reorganise surface materials, substrates are often very different from pre-mining operations, and restoration trajectories often stall at a certain point along a successional pathway (Doherty 1998). For example, surface compaction and erosion of reconstructed soils after mining can suppress the development of tree species and forest cover (Macdonald et al. 2015; Sweigard et al. 2007). Similarly, a dense cover of non-native grass and fern species stalled the regrowth of tree canopy on abandoned farmland in eastern Australia (Liangzhong and Whelan 1993). In many cases, the landscape complexity and soil conditions of the reference ecosystem have developed slowly through time, and recreating important abiotic processes within the timeframe of restoration projects may be impossible. Ecosystems such as tall forests can be structurally and functionally complex with a high diversity of plant species and long-lived dominant species, and re-establishing such complexity is also often beyond our capabilities (Macdonald et al. 2015). Restoration to ’original’ conditions may be considered impossible, and the only alternatives are rehabilitation or construction of a new ecosystem that functions differently (Aronson et al. 1993; Hobbs and Norton 1996).

Mining often presents a need for complete rehabilitation of biological communities (Macdonald et al. 2015), hence intimate knowledge of local plant species and habitat requirements of fauna are pertinent for this kind of disturbance. Perhaps the greatest challenges to restoration, however, derive from the unsuitability of much of the mined overburden soils for plant growth (Carrick and Krüger 2007). Severe changes in the distribution of soil properties following mining activities usually impedes the recruitment of slow-growing shrub and tree species (Martínez-Garza et al. 2013; Morrison et al. 2005; Paul et al. 2010). Soil reconstruction after mining can also increase course particle content in topsoils (Román-Dañobeytia et al. 2015), which may reduce the water storage capacity of soils to levels insufficient to support germination or plant growth (Binkley and Fisher 2013). Understanding soil properties that drive ecohydrological function is key to improving restoration outcomes in arid zones (Luna et al. 2018). Climate cannot be controlled but water availability and redistribution, as well as evapotranspiration demand, can be managed through the spatial arrangement of soils, vegetation cover and connectivity in the rebuilt landscape (Macdonald et al. 2015).

Mineral sand mining occurs in every state across Australia, making the country the world’s leading supplier of mineral sands (WA Govt 2019). Mine-site rehabilitation is a legal obligation for all mining projects in Australia and rehabilitation must, at the very least, be designed to meet three key objectives: 1) the long-term stability and sustainability of the landforms, soils and hydrology, 2) the full, or partial, repair of ecosystem capacity to provide habitats for biota and services for people, and 3) the prevention of pollution of the surrounding environment (Aust Govt 2016). Full repair of ecosystem function and stability is often difficult to achieve for restoration projects in arid zones, due to the harsh environmental conditions. Given our existing knowledge gaps about how severe disturbance impacts ecosystem function, and recruitment dynamics in uncultivated species, further research and some refinement of rehabilitation operations may be necessary (Grant et al. 2016).

1.7 VEGETATION DYNAMICS AT THE STUDY SITE

Mineral sand mining occurs approximately 30 km west of Pooncarie, in far southwest New South Wales, and rehabilitation of mined sites has been underway since 2006. The mine sites are located amongst semi-arid sand plain woodlands and chenopod shrublands, although mallee woodlands appear as small, scattered populations surrounding the mine sites (Figure 1.2; OEH 2019). Prior to mining, the three major plant community types were Pearl bluebush shrubland (Fig 1.3a), Belah-Pearl bluebush woodland and Belah-Rosewood woodland (Fig 1.3b), as described by Benson et al. (2006). Restoration efforts have resulted in the establishment of important native shrubs, however tree species have proven very difficult to re-establish. Sporadic rainfall and high temperatures, which greatly influence the reproduction and survival of tree species (Bi et al. 2014; Padilla et al. 2009; Will et al. 2013), along with limited seed supply, complicate the restoration process.

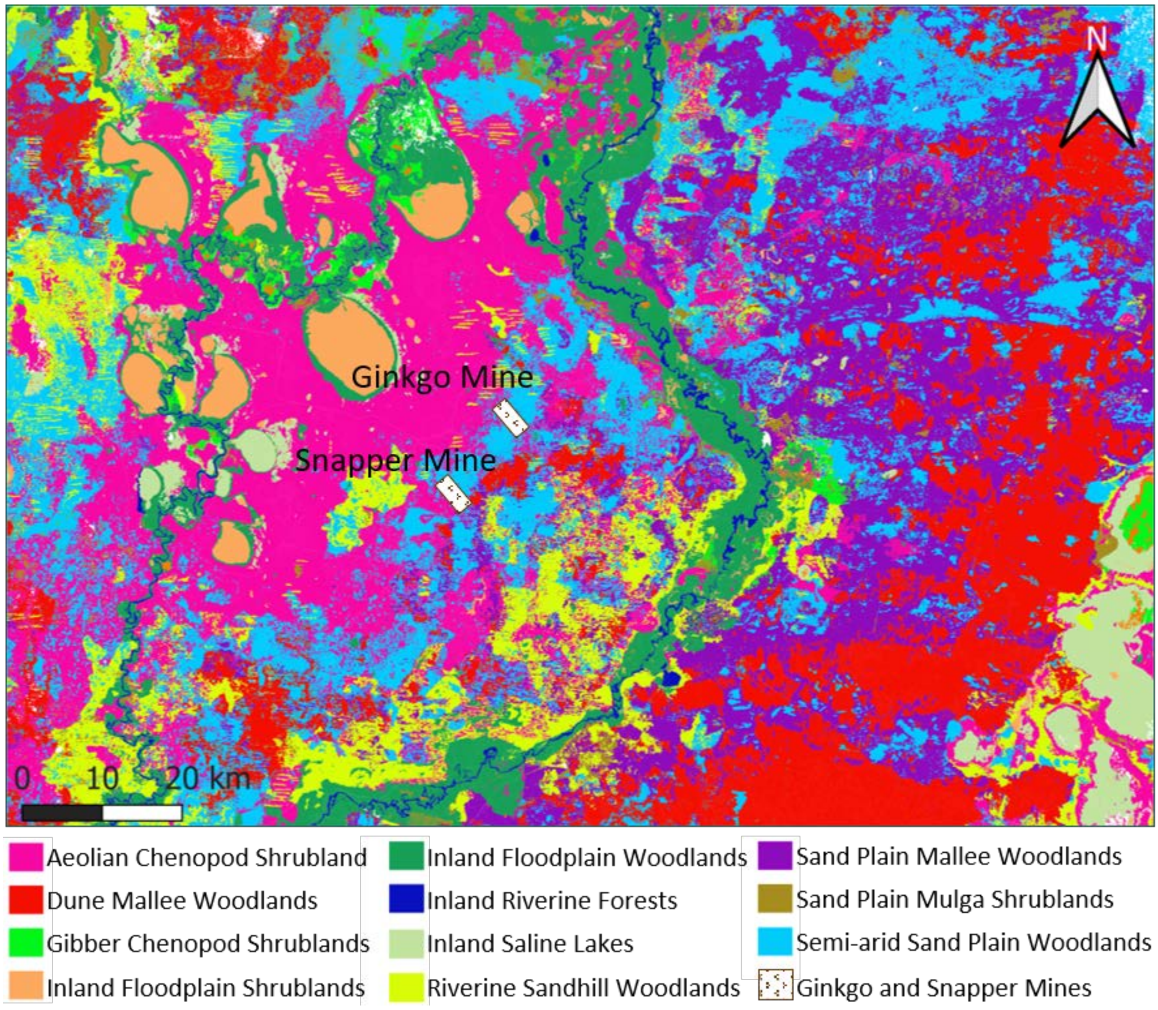

Fig 1.2: Vegetation types at the study site were classified as Aeolian Chenopod Shrublands, specifically Pearl bluebush shrubland, and Semi-arid Sand Plain Woodlands, dominated by tree species, *Casuarina pauper* and *Myoporum platycarpum*. Source: Map layer was provided by the State of New South Wales and Office of Environment and Heritage (OEH 2019), and produced using QGIS 3.6.3.

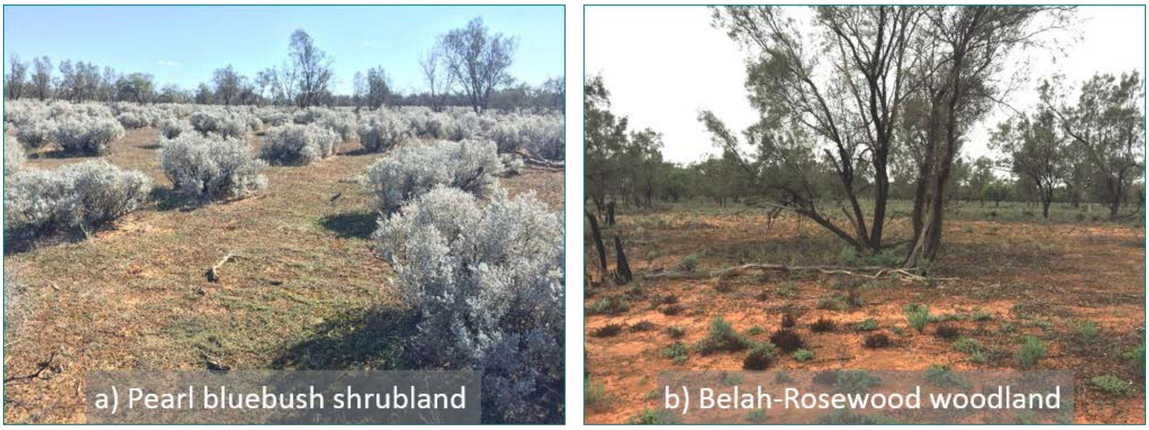

Fig 1.3: Remnant vegetation prior to disturbance was classified as (a) Pearl bluebush shrubland, (b) Belah-Rosewood woodland, or an ecotone between these two sites of Belah-Pearl bluebush woodland.

Rainfall and temperature patterns at the study site are highly variable, largely influenced by El Niño and La Niña events (BOM 2014). The study area is arid, or a hot desert climate, according to the Koppen Classification System. Rainfall at the study site is highly variable and unpredictable. Mean annual rainfall is 250 mm across 60 years of climate data collected from Pooncarie, which is 30 km east of the study site (BOM 2018; Fig. 3a), although average annual rainfall can often fall below 200 mm for consecutive years (Environdata 2019). Temperatures can exceed 47°C, though mean monthly temperatures range from 4°C to 36°C (BOM 2018). Evaporation rates are significantly higher than rainfall in all months (Environdata 2019) and, unlike most arid zones across the globe (e.g.; Fig 1.4b), there is no predictable wet season, which further complicates the restoration process.

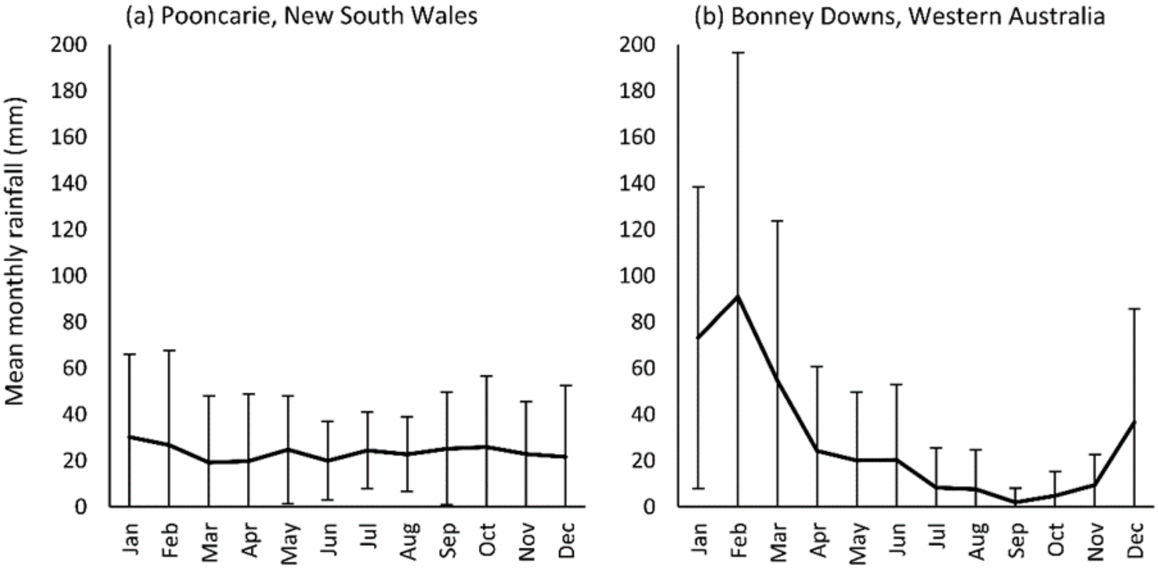

Fig 1.4: Mean monthly rainfall, from 1956-2016 (BOM 2018), at the study site (a) has no wet season, whereas most other arid zones have a predictable wet season (b; Bonney Downs, WA is an example of typical rainfall patters of arid zones).

This research focuses on two existing mines in far southwest NSW, Ginkgo and Snapper Mines, which extract heavy minerals by wet dredging (Fig 1.5). Ginkgo and Snapper Mines will disturb approximately 5000 hectares of native woodland, and similar mines have recently been approved across the region. Mineral sand mining commenced at the Ginkgo Mine in January 2006 and, with the longest restoration history, the Ginkgo Mine is the focus of this research. Both mine sites, and the recently approved additional mine sites in the region, adhere to the same mining and restoration protocols demonstrated in Fig 1.6 (Cristal Mining 2013; Cristal Mining 2015a). Vegetation is cleared, topsoil is stripped and stockpiled (or directly returned when possible), subsoil is then stripped and stockpiled and the subsoil and topsoil are returned in reverse order of stripping onto former mined areas. Soil stripping and return is performed using GPS guided, laser scoop buckets, allowing for accurate depth control in stripping. As the dredge vessel progresses along the mine path, the mine is progressively backfilled and rehabilitated. The excess soil from reduced compaction creates overburden stockpiles that remain as permanent and mountainous features of the landscape. After shaping, these overburden stockpiles, soil stockpiles and mine path areas, are rehabilitated using an average of 20 cm of subsoil and a minimum of 20 cm of topsoil above the subsoil (Sluiter and Schultz 2017). This equates to a loss of approximately 10 cm of topsoil in the mining process (Cristal Mining 2015a), likely due to soil disturbance and erosion (Sheoran et al. 2010). Revegetation by direct seeding with indigenous species occurs between autumn and early winter, when evaporation rates are lower.

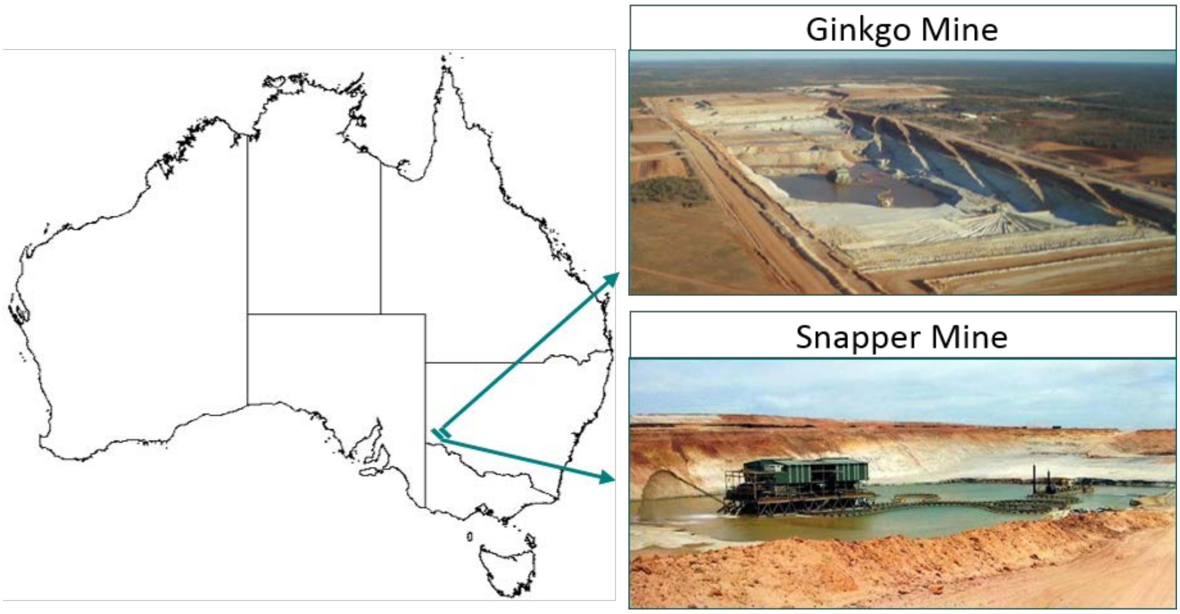

Fig 1.5: Site location of Ginkgo and Snapper Mines, which combined disturb approximately 5000 ha of native arid woodlands and shrublands. Source of images: Ginkgo Mine (Cristal Mining 2013) and Snapper Mine (Cristal Mining 2012).


a) Belah-Bluebush Woodland
b) Vegetation cleared by chaining
c) Soils removed & dredging begins
d) Soils replaced with laser scoops
e) Direct seeding with drum seeder
f) Perennial vegetation established
g) Six years since restoration with remnant ecosystem in the background

Fig 1.6: Mining and restoration processes at site location: The mining process begins as a native belah bluebush woodland (a). Vegetation is cleared by the chaining method, which drags vegetation from the landscape (b). Topsoil and subsoil are stripped and stored separately, and mineral extraction begins with floating dredges that move along each orebody strike (c). Tailings and overburdens are progressively back-filled in to the mined void behind the mining face. Soils are replaced (and removed) with accuracy using GPS guided laser scoops (d). Revegetation occurs between autumn and early winter, and relies on direct seeding of local provenance species (e) as well as planting of tubestocks. Perennial vegetation establishment occurs rapidly (f: Ginkgo Mine rehabilitation 27 months after seeding), but long term results (g) show poor recruitment of keystone tree and shrub species. Tree trunks in final restoration picture (g) are dead trunks installed for bird habitat. Source of images: a (Sluiter et al. 2014), b (Mills and Minns 2017), c (Cristal Mining 2013), d, e and f (Sluiter 2012).

Four different seeding techniques are implemented for the sowing of native seed: a large drum seeder mounted to dozer rippers, a drum seeder attached to agricultural ploughs, a precision tree seeder for species including *Alectryon oleifolius*, *Myoporum platycarpum* and *Casuarina pauper* (respectively seeded at a rate of 50, 100 and 200 g/ha, assuming sufficient seed supply), and grass seeding by hand broadcasting or using a wire frame attached to a utility vehicle (Fig 1.7; Cristal Mining 2018a). Chenopod plant species, *Atriplex* and particularly *Maireana pyramidata*, are the most successful species from seeding efforts, while tree species in the seed mix perform particularly poorly. Consequentially, tree species have recently been removed from the seed mixture, which primarily consists of chenopods, sown at a rate of ~12 kg/ha (Cristal Mining 2018b). To improve tree recruitment, large numbers of tube stocks were planted and irrigated for a short period of time, although recent drought conditions have caused poor survival rates of tubestocks, and seeds, planted within the last three years (Sluiter and Schultz 2017). To date, it has been difficult to reinstate the trees which characterize the surrounding landscape and hand-planting, aided by drip irrigation, has given the best result (Sluiter and Schultz 2017). Rainfall immediately post-seeding results in greater plant recruitment (Cristal

Mining 2018a) however, as there is no wet season, it is difficult to plan and implement restoration to coincide with rainfall at this site.

Fig 1.7: Four different seeding techniques implemented at the Ginkgo mine site: (a) a large drum seeder mounted to dozer rippers, (b) a tractor with an agricultural plough and drum seeder, (c) a precision tree seeder attached to a utility vehicle and (d) grass seeding by hand broadcasting or using a wire frame attached to a small utility vehicle (images from Cristal Mining 2018a).

Revegetation monitoring conducted in 2017 and 2018 at the study site report distinct successional changes in plant taxa with time since seeding, from predominantly short-lived species during the initial years to longer-lived perennials after three years since seeding (Sluiter and Schultz 2017; Sluiter and Schultz 2019). Many studies suggest that annuals and small shrubs facilitate the recruitment of some perennial species, acting as nurse plants that provide shelter and nutrients in otherwise barren landscapes (Dalotto et al. 2018; Navarro-Cano et al. 2015; Padilla and Pugnaire 2006). Although some perennial species may benefit from nurse plants, weeds appear to inhibit the recruitment of many perennials at the study site (Cristal Mining 2015b; Sluiter and Schultz 2017). For example, at least one restoration site is considered to have failed, with very little native species recruitment, due to an infestation of Ward's Weed (*Carrichtera annua*) after three years since seeding (Sluiter and Schultz 2017). Furthermore, weedicide application prior to seeding results in major improvements to native shrub cover (Sluiter and Schultz 2017).

Restoration success is highly variable between sites, although most sites are characterized by lower native shrub presence and plant cover than the desired benchmark (Sluiter and Schultz 2017). The desired benchmark of ~25% of the landscape covered with native plants has been difficult to achieve (Sluiter and Schultz 2017), particularly during drought. For example, vegetation monitoring reports the cover of seeded species rose to 27% after three years, and it appeared the restoration was heading in the right direction, however cover of seeded species dropped to 16% during drought conditions (Sluiter and Schultz 2019). As plant cover can fluctuate wildly at restoration sites, the long-term sustainability of the reconstructed system is uncertain.

Restoration of mine path and soil stockpiles is generally more successful than overburden sites (Cristal Mining 2015b), possibly due to increased exposure to wind at overburden sites, which remain as large, mountainous structures across the landscape that have steep edges prone to soil erosion. Low rainfall, high temperatures and wind exposure are considered the greatest risks to successful restoration at the study site, and secondary significant risks include limited topsoil supply, additions of salts and browsing by wildlife (Cristal Mining 2016). Recruitment of native species improves significantly when seeding coincides with large rainfall events, however high rainfall also increases invasions of weed species (Sluiter and Schultz 2017). Current drought conditions have caused significant germination failures from seeding efforts, and chenopod species that had successfully established at older restoration sites are showing signs of moisture stress, such as defoliation and dieback (Cristal Mining 2018a; Sluiter and Schultz 2017). The restoration goal is to restore self-regenerating vegetation types comprised of indigenous plant taxa in vegetation community types similar to those occurring in surrounding areas (Cristal Mining 2015a), which has not yet been achieved despite significant restoration efforts.

1.8 RATIONALE AND AIMS

This thesis explores the complex interactions among rainfall, soil properties and plant recruitment strategies in arid zones, and the impact of mining and subsequent restoration on these dynamics. One key theme runs throughout my thesis: that water is the most important limiting resource to biological production and seed germination in arid zones. Rainfall is an important determinant of community dynamics in arid zones (Noy-Meir 1973; Reynolds et al. 2004; Schwinning and Sala 2004) and the temporal and spatial availability of water from rainfall events are governed by soil properties (Rodriguez-Iturbe et al. 1999; Schwinning et al. 2004), thus soil reconstruction can affect plant regeneration (Maestre et al. 2003). Seeds have critical water thresholds and, when available water falls below physiological thresholds for seed germination for an extended period of time, major recruitment losses can be expected. Recruitment from seed can be enhanced, and seed mortality reduced, by understanding physiological thresholds for germination (Ruthrof et al. 2013) and by ameliorating abiotic conditions that limit germination and plant recruitment (Ruthrof et al. 2010). Seeds need water to germinate, and water availability in arid ecosystems is very much linked to soil structure and organisation, hence this thesis investigates both of these elements.

Our poor knowledge of dormancy cues and seed storage behaviour for many native species used in arid restoration projects is often cited as a key factor limiting our ability to achieve greater restoration success (Gross and Mackay 2014; Merritt and Dixon 2011; Rokich and Dixon 2007). Woody plants that were dominant in the pre-existing landscape at this study site, and that are difficult to recruit after mining, include eight ecologically important tree and shrub species; (1) *Casuarina pauper*; (2) *Myoporum platycarpum* ssp. *platycarpum*; (3) *Geijera parviflora*; (4) *Alectryon oleifolius* ssp. *canescens*; (5) *Hakea tephrosperma*; (6) *Atriplex rhagodioides*; (7) *Maireana sedifolia*; and (8) *Maireana pyramidata*. Therefore, these species constitute the focus of seed related studies in this thesis. This thesis explores seed traits, and soil properties, important for the restoration of arid ecosystems, using the following framework which appear as four separate chapters (Fig 1.8).

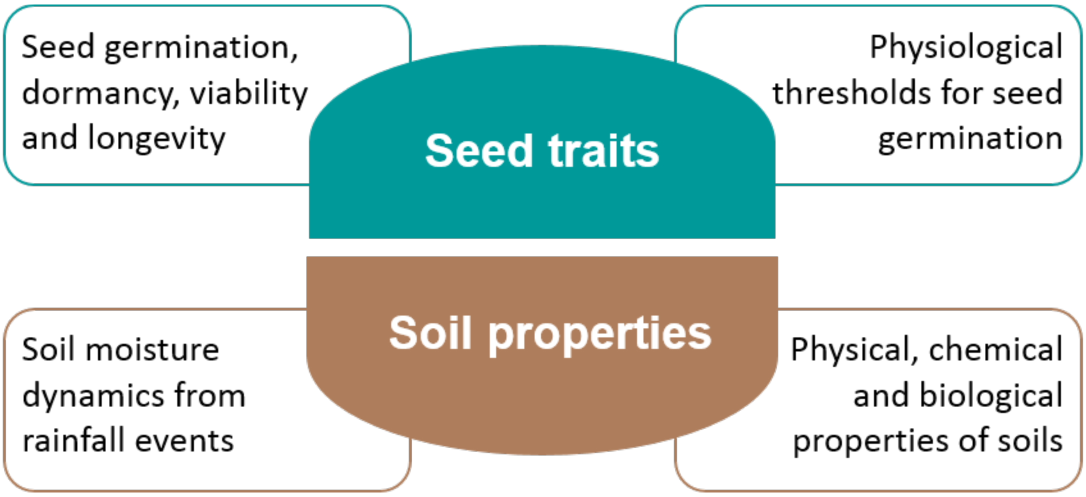

Fig 1.8: Thesis setup and chapter outline, born from the hypothesis that water is the most important limiting resource to biological production and seed germination in arid zones, and that disturbing the soil profile effects moisture retention and impedes regeneration.

This is the first study to explore the ecophysiology of seeds from an arid zone with no predictable wet season, hence seed responses were difficult to predict. Furthermore, it is the first study to measure the real-time, temporal fate of water from rainfall events, in an arid zone during one of the longest droughts in history. Consequentially, it challenges our previous assumptions about the types of rainfall events deemed biologically significant for the regeneration of woody plant species. Studies such as this, which explore potential reasons for the poor success rates of arid ecosystem restoration, are urgently required to improve recruitment across novel landscapes. Results from this study highlight how seed traits, and the regeneration strategies of species, interact with microsite conditions, and provides vital information to predict how arid species may respond to land-use change and restoration management approaches.

1.9 THESIS OUTLINE

The main research areas presented in this thesis follow the outline below. Each chapter has been, or will be, submitted as scientific papers for publication, which means that there is some unavoidable duplication of introductory and study site information in the following chapters. Chapters 2 and 3 focus on seed traits and germination strategies important to arid species, and chapters 4 and 5 reveal how reconstructed soils compare to pre-existing soil condition, particularly in properties important for plant development. Chapter 6 is a synthesis and discussion of the research, and explains how these findings can be used to improve the management of arid ecosystems.

Chapter 2: *Lower dormancy with rapid germination is an important strategy for seeds in an arid zone with unpredictable rainfall.*

This chapter explores the germination strategies of seeds that facilitate survival in harsh environments, and discusses seed morphology and physiology. Here, I investigate the ecology of seed dormancy, germination and longevity, to test assumptions about the prevailing seed traits of species from arid environments. This study has implications for the restoration of an arid ecosystem and highlights germination and seed characteristics that may be favourable regeneration traits in reconstructed systems.

Chapter 3: *The risk-takers and avoiders: germination sensitivity to water stress in an arid zone with unpredictable rainfall.*

This chapter assesses the role of water availability and temperature in the germination strategies of keystone arid-zone plant species. Compared to species from other arid regions with predictable wet seasons, all species in this study were considered water-stress sensitive, with high moisture thresholds for germination. This study provides insights into the complex interaction between water, temperature, plant recruitment and community dynamics in arid zones.

Chapter 4: *Soil reconstruction after mining fails to reinstate properties crucial for vegetation recovery in arid Australia.*

The aim of this chapter is to assess soil structure in differing vegetation types within the pre-existing, productive arid ecosystem, and to understand how these soil properties are impacted by mining. Reclamation of mined lands can be managed more effectively when the biophysicochemical properties of soils have been assessed, and methods to ameliorate conditions unfavourable for plant growth are considered in restoration plans.

Chapter 5: *Reconstructed soils have a lower soil moisture response than remnant systems after rainfall events.*

Here, I investigated the mechanics of how rainfall events translate to soil moisture and ecosystem function in arid ecosystems in their remnant state, and in reconstructed soils. This study provides unique and quantitative insights into the complex relationship between soil moisture and the different types of rainfall events commonly observed in arid zones, and highlights the importance of incorporating methods to reduce evaporative water loss in reconstructed soils.

Chapter 6: *Synthesis and implications for management*

This chapter summarises the key barriers to restoration in disturbed, arid ecosystems and highlights the importance of restoring ecohydrological processes to improve arid restoration. I discuss the implications of my research for the management and restoration of species in this study, and arid ecosystems in general. Understanding biotic and abiotic factors limiting plant recruitment and development presents informed opportunities to improve restoration outcomes and predict plant responses to management approaches.

CHAPTER 2

Lower dormancy with rapid germination is an important strategy for seeds in an arid zone with unpredictable rainfall

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2.1 ABSTRACT

Seed germination traits are key drivers of population dynamics, yet they are under-represented in community ecology studies, which have predominately focussed on adult plant and seed morphological traits. We studied the seed traits and germination strategy of eight woody plant species to investigate regeneration strategies in the arid zone of eastern Australia. To cope with stochastic and minimal rainfall, we predict that arid seeds will either have rapid germination across a wide range of temperatures, improved germination under cooler temperatures, or dormancy and/or longevity traits to delay or stagger germination across time. To understand how temperature affects germination responses, seeds of eight keystone arid species were germinated under laboratory conditions, and under three diurnal temperatures (30/20°C, 25/15°C and 17/7°C) for 30 days. We also tested for decline in seed viability across 24 months in a dry-aging treatment (~20°C). Six of the eight arid species studied had non-dormant, rapidly germinating seeds, and only two species had physiological dormancy traits. Seed longevity differed widely between species, from one recalcitrant species surviving only months in aging (P50 = < 3 months) and one serotinous species surviving for many years (P50 = 84 months). Our results highlight the importance of understanding the reproductive strategies of plant species in arid environments. Rapid germination, the dominant seed trait of species included in this study, allows arid species to capitalise on sporadic rainfall. However, some species also exhibit dormancy and delayed germination; this an alternative strategy which spreads the risk of germination failure over time.

2.2 INTRODUCTION

Seed traits and germination strategies drive plant community dynamics and provide insight into species' adaptations to environmental filters (Larson and Funk 2016) and community composition (Guo et al. 2000). Despite this, seed traits are under-represented in community ecology studies (Kleyer et al. 2008; Pérez-Harguindeguy et al. 2013; Wagner et al. 2014). Knowledge of seed traits and germination strategies is necessary to describe plant niches, to anticipate population dynamics under changes in land use (Saatkamp et al. 2019), and to assess plant responses to the environment (Kleyer and Minden 2015). By studying seed traits and germination responses we can obtain ecologically meaningful data about the functional properties of plant communities that improve predictions of plant assemblages under natural, and anthropogenic, environmental change (Jiménez-Alfaro et al. 2016).

Seed traits and germination strategies, which are often unrelated to other plant traits (Pierce et al. 2014), can inform us about the reproductive strategies of species occurring in particular environments (Huang et al. 2016b). Seed mass is the most widely studied seed trait, and there are strong correlations among seed mass, germination rate, survival and establishment (Moles and Westoby 2004; Norden et al. 2008). Small seeds generally germinate faster than heavy seeds (Gomaa and Picó 2011), however the chance of survival and establishment at the seedling or later plant stages is greater for heavier seeds (Baraloto et al. 2005; Westoby et al. 1992). Furthermore, small-seeded species are generally able to produce more seeds (Westoby et al. 2002). Physiological responses of seeds to environmental cues enable germination to occur when conditions are most suitable for seedling establishment (Long et al. 2015; Saatkamp et al. 2014). Conversely, seedling mortality can increase if germination occurs in unfavourable environmental conditions; thus germination timing has strong fitness consequences (Donohue 2005; Hoyle et al. 2015; Simons and Johnston 2000).

The primary abiotic filters for recruitment of most arid plant species are water availability and the season it occurs in, and seeds of arid zone plants typically exhibit adaptive traits to tolerate or avoid drought conditions (Al-Shamsi et al. 2018; Zeng et al. 2010). Rainfall events that last several days are rare in arid zones, and smaller rainfall events are likely to result in the drying of upper soil layers before the germination process is complete (Choinski and Tuohy 1991), causing seedling mortality after germination. Conversely, a rainfall event during winter may present slower evaporation rates from the soil surface than during summer. Hence, for species that rely on avoidance strategies to survive drought conditions, the timing of recruitment must coincide with periods of reliable soil water availability (Salazar et al. 2011). Dormancy is an important drought avoidance mechanism for arid species as it restricts germination during unsuitable environmental conditions (Poschlod et al. 2013), whereas rapid germination is a drought tolerance strategy to facilitate the rapid exploitation of temporarily favourable conditions (Grime et al. 1981). The evolution towards mature seeds with less nutritive tissue available to the embryo has enabled seeds to germinate faster (Vandelook et al. 2012; Vivrette 1995) and emerge when rainfall events are short.

The level of seed dormancy can vary among seeds within a population so that germination of individuals occurs over several seasons (Commander et al. 2017; Gremer et al. 2016; Lewandrowski et al. 2018). This reproductive strategy has been termed bet-hedging, as it limits synchronous germination events, spreading the risk of germination failure across seasons. This increases long-term fitness by preventing the mortality of the entire seed cohort during unfavourable conditions (Tielbörger et al. 2012), provided seeds survive through multiple seasons of unfavourable conditions. Hence, dormancy and longevity are key traits of bet-hedging. However, in unpredictable environments, selection may favour plants that can reproduce rapidly and frequently, and hence bet-hedging may be less prevalent.

In arid ecosystems, Baskin and Baskin (2003) estimate that 85% of plant species produce dormant seeds. The prevalence of dormancy generally increases with aridity (Volis and Bohrer 2013), but the influence of rainfall predictability on seed traits is not as well studied. Modelling by Brown and Venable (1986) predicts that the prevalence of dormancy traits should increase with decreasing rainfall predictability. Conversely, Harel et al. (2011) found that dormancy decreased with rainfall predictability in desert annuals, hence further studies are required to ascertain the prevalence of seed dormancy in relation to aridity. Seeds of arid zone plants are often characterised by faster germination rates than those from regions of higher rainfall (Bochet et al. 2007; Jurado and Westoby 1992), after dormancy is overcome. Species that germinate quickly are able to utilise the short pulses of water availability, reducing the likelihood of seed mortality (Parsons 2012), while the seedlings of slower-germinating species may be limited to using dwindling water availability at the end of longer rainfall pulses (Chesson et al. 2004). Further empirical evidence is required from a greater suite of species (particularly perennials), and from a greater range of environments, to test the effect of rainfall predictability on seed traits and to determine the prevalence of dormancy in the arid zone.

This study investigates the seed traits and germination strategy of eight Australian, arid zone species. The species selected are considered as keystone plants, as they are the dominant species and the only prevalent woody species in the ecosystem. We focused on traits that may be critical to species' persistence in arid ecosystems, and that are essential to understand if we are to successfully restore these species using seed. We hypothesise that seeds will be categorised by one of three strategies beneficial to recruitment in arid zones. To cope with stochastic and low rainfall, we predict that species adapted to the arid zone produce seeds that will either 1) have low seed mass but with rapid germination, across a wide range of temperatures, to ensure seedling establishment before soil moisture evaporates, 2) show improved germination under cool, winter temperatures where soil evaporation rates are lowest, or 3) have dormancy and/or longevity traits to delay or stagger germination, therefore spreading the risk of germination failure across time. Specifically, we measure seed dormancy and embryo traits, germination responses under different temperature regimes, and seed longevity under ambient aging conditions. We also test if seed mass, and other traits, are related to germination strategy and whether seed traits can be used as a proxy for germination strategy. We highlight important germination strategies of plants from an arid zone with stochastic rainfall, and discuss the evolution of seed traits that favour seed survival and germination when rainfall is infrequent and unpredictable.

2.3 MATERIALS AND METHODS

2.3.1 Study species and seed collection

We chose the following Australian arid zone species for this study: trees *Casuarina pauper* F.Muell. ex L.A.S.Johnson (Casuarinaceae)*, Myoporum platycarpum* ssp. *platycarpum* R.Br., *Geijera parviflora* Lindl. (Scrophulariaceae), *Alectryon oleifolius* ssp. *canescens* S.T.Reynolds (Sapindaceae) and *Hakea tephrosperma* R.Br. (Proteaceae), and understory shrubs from the Chenopodiaceae family, *Atriplex rhagodioides* F.Muell.*, Maireana sedifolia* (F.Muell.) Paul G.Wilson and *Maireana pyramidata* (Benth.) Paul G.Wilson. All species in this study are targeted for restoration after mineral sand mining. Vegetation communities prior to clearing include three major plant community types; shrublands dominated by *M. sedifolia*, woodlands dominated by

C. pauper and *M. platycarpum* and woodlands with shrubland understory, dominated by *C. pauper* and understory shrubs *M. sedifolia* and *M. pyramidata* (Sluiter and Schultz 2017). Less dominant tree species occur as small, scattered patches across the landscape and include *H. tephrosperma*, *A. oleifolius* and *G. parviflora*.

The climate of the study area is arid (250 mm mean annual rainfall) although average annual rainfall can often fall below 200 mm for consecutive years. Temperatures range from 2°C to 47°C, with cooler mean daily temperatures from May to August (Fig. 2.1; BOM 2018). Across 60 years of climate data, average monthly rainfall was 24 mm and, unlike most arid zones across the globe, there is no distinct wet season (BOM 2018).

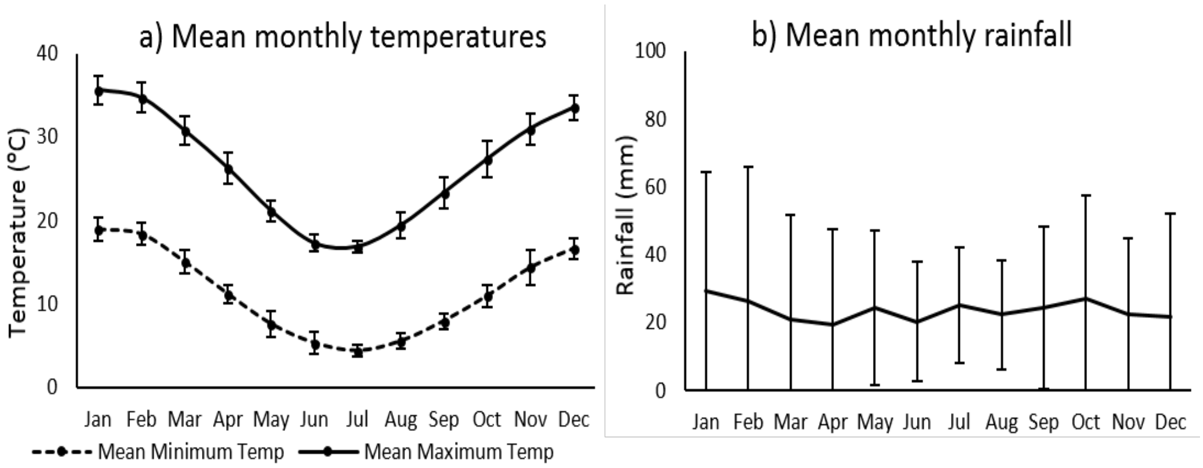

Fig 2.1: (a) Mean monthly minimum and maximum temperatures from 2003-2016, and (b) mean monthly rainfall, from 1956-2016, at the study site. Unlike most other arid zones, there is no predictable wet season.

Mature seeds of each species were collected from remnant populations adjacent to a mine site (33°22’05”S, 142°13’36”E) at which restoration of these species is planned, however, for species with infrequent seeding events (*H. tephrosperma*, *A. oliefolius* and *A. rhagodioides*), seeds were collected within a 200-km radius of the mine site. Seeds were either collected by hand, donated from Ecotypic Pty Ltd and Tronox Mining, or purchased from Ogyris Pty Ltd. Where possible, seeds were collected within the six months prior to testing. However, due to lack of seeding events, it was necessary to use seeds stored for over one year in some species (seed ages shown in Table 2.1). Seeds were manually cleaned and stored in paper bags, under cool dark conditions. Bracts and seed covering structures were removed prior to seed weight measurements and germination experiments.

2.3.2 Seed traits: embryo type, mass, viability and imbibition

For each species, the ratio of embryo length to seed length (E:S) was calculated based on longitudinal dissections and measurements of 50 fully-imbibed seeds (Baskin and Baskin 2007). Seed viability was assessed in a 1% solution of 2,3,5-triphenyl tetrazolium chloride (TZ), except for *H. tephrosperma*, for which seeds were incubated on moist filter paper at 30/20°C due to consistently poor TZ stain results; they gave a germination response of 100%. Embryos that only partially absorbed stain were scored as weakly viable (Fig 2.2a-c) and were classified as non-viable seeds. To ensure accurate TZ interpretations, results were frequently compared to tests for viability by germinating seeds at diurnal temperatures at 30/20°C, and according to the germination methods outlined below. Seed mass was determined using the mean of three replicates of 100 seeds, with results then divided by 100 to represent weight (g) per seed.

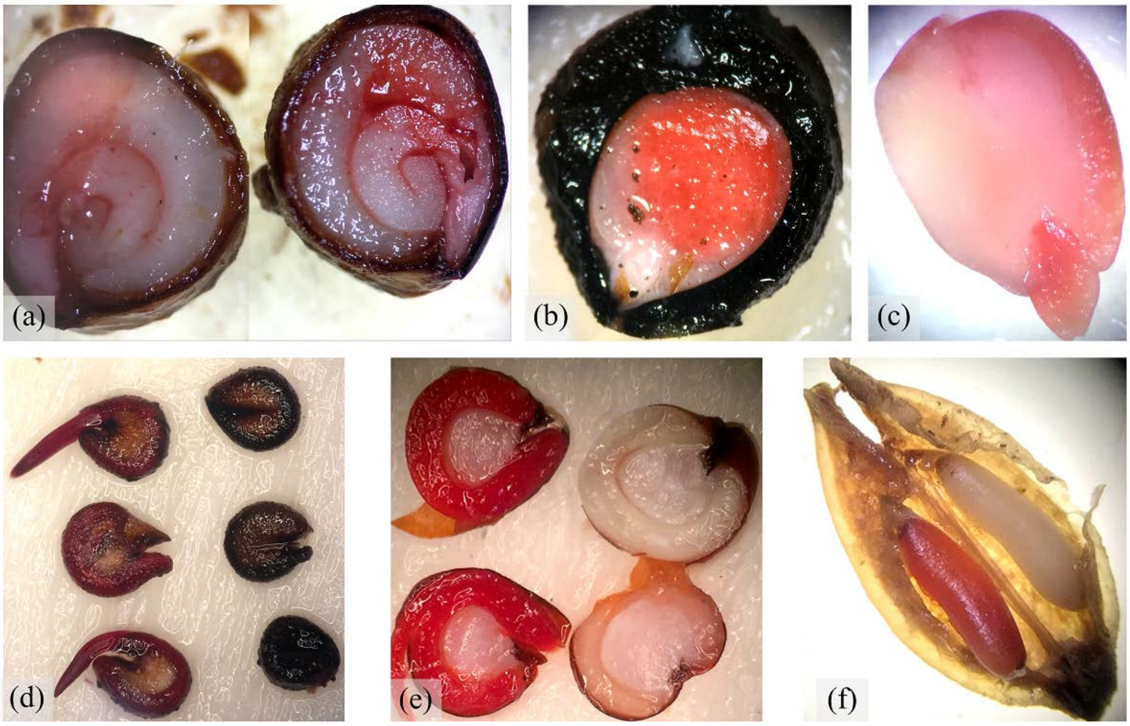

Fig 2.2: Microscope images of TZ stained seeds for viability tests, including (a) *A. oleifolius*, (b) *G. parviflora*, (c) *C. pauper*, (d) *M. pyramidata*, (e) *A. rhagodioides*, and (f) *M. platycarpum*. Weakly viable seeds were only partially stained and considered not viable (a-c). Seeds with viable embryos stained red (left in images d-f) and unviable embryos remained unstained (right-hand-side in d-f).

For imbibition tests, four replicates of 25 seeds were weighed, placed on moist filter paper, and incubated under three diurnal temperatures of 30/20°C, 25/15°C and 17/7°C, under a 12 hr light/dark schedule. Seeds were weighed when dry at beginning of experiment and, after 5 min on moist filter paper, seeds were removed and patted dry with a paper towel to absorb surface moisture, and weighed. To determine increases in seed weight, seeds were re-weighed at 10 min, 30 min and at 1, 2, 3, 6, 9, 24, 48, 72, 96, 120, 144, 168 and 192+ hrs. All bracts and seed coverings were removed for imbibition, germination and viability tests, but they were retained for the longevity experiment as this is how seeds are currently stored after collection. For one species (*G. parviflora*), additional tests were performed in an attempt to alleviate dormancy, including the move-along method (as described by Baskin and Baskin 2014)and soaking in boiling water and 90% H_2SO_4, both treatments for 1 min, 30 min and at 1, 4, 12, 24 and 48 hours.

2.3.3 Germination responses under diurnal temperatures

Prior to germination treatments, seeds of all species were surface sterilised by soaking in 1% sodium hypochlorite for one minute, then rinsed for 40 seconds with double distilled water. For each species, four replicates of 25 seeds each were used. Seeds were placed in 90-mm diameter petri dishes on filter paper moistened with distilled water and incubated at a 12/12-hr light/dark regime at daily alternating temperatures of 30/20°C, 25/15°C and 17/7°C). Seeds were incubated in cabinets (Thermoline Scientific, temperature and humidity cabinet, Model: TRISLH-495-1-s.d., Vol. 240, Sydney, Australia) under cool-white fluorescent lamps with a 40 µmol.m^{-2} photosynthetic photon flux. To determine the effects of gibberellic acid (a plant hormone herein referred to as GA_3) on seed germination, species were incubated at 30/20°C and the filter paper was moistened with a 350 ppm GA_3 solution. To prevent microbial outbreak and ensure constant hydration during germination tests, seeds were transferred to sterilised Petri dishes weekly, on new filter papers moistened with the same appropriate water/GA_3 solutions. Seed germination (when the radicle emerged to at least half of seed size) was recorded daily for 30 days, or until germination ceased for four consecutive readings across all treatments. For two species that exhibited dormancy traits (*G. parviflora* and *A. rhagodioides*) an after-ripening treatment was applied by storing seeds for one year, under constant dark and air-conditioned temperatures between 10–20°C and 45–50% humidity. An additional four replicate plates at each diurnal temperature were included for both of these species using the after-ripened seeds. Seeds for the treatments with and without after-ripening were from the same seed lot.

2.3.4 Longevity

Seed longevity was assessed to understand the relationship between longevity and dormancy classification. Seeds of species in this study are currently collected for restoration purposes and stored at the study location in air-conditioned shipping containers at ~20°C, hence we tested the effects of these aging conditions on seed longevity. Seeds were manually cleaned to remove excess organic matter from the seed batch, and stored in paper bags, under constant dark and air-conditioned temperatures between 10–20°C and 45–50% humidity. Temperature and humidity of aging treatments were monitored and recorded once a fortnight for 24 months. To test for viability loss with aging, 100 seeds were extracted at 0, 3, 6, 12, 18 and 24 months, and TZ stained as per viability testing methods listed above. Due to seed shortages in *A. oleifolius*, only 60 seeds were tested for viability at each longevity test.

2.3.5 Data analysis

Imbibition was calculated using increase in seed weight after 72 hours:

$$\mathrm{I72} = [(W_i - W_d)/W_d] \times 100$$

where W_i is mean mass of imbibed seeds and W_d is mean mass of dry seeds (Turner et al. 2006). Viability of seed batches was tested in the days prior to experiment, and Viability-Adjusted Germination (VAG, herein referred to as germination) was calculated using the following equation (Sweedman and Merritt 2006):

$$\mathrm{VAG} = \frac{\text{Final germination (\%)}}{\text{Mean viability (\%)}} \times 100$$

For each replicate dish, the time to minimum germination (t_{min}) was taken as the first day that germination was observed, time to 50% germination (t_{50}) was the first day that germination was recorded at ≥50%, and time to maximum germination (t_{max}) was the first day at which the maximum germination was recorded. Mean t_{min}, t_{50} and t_{max} were calculated from the four replicates of each species at each diurnal temperature. Loss of seed viability with aging was calculated as:

$$V_{loss} = \frac{\overline{V_1} - \overline{V_2}}{\overline{V_1}}$$

where $\overline{V_1}$ is mean viability at day 0, and $\overline{V_2}$ is mean viability at day of test. A Pearson test was used to test the correlation between seed weight and t_{50}, longevity (P50) and seed fill, and between embryo type (ranked according to E:S) and t_{50}. One-way ANOVAs were used to test the effects of diurnal temperatures on maximum germination and t_{max}. Shapiro-Wilk tests confirmed the normality of both maximum germination and t_{50} data prior to ANOVAs. Tukey HSD post-hoc tests were used to make multiple comparsions of means among diurnal temperature treatments. Welsh's t-tests were performed to compare germination between water and GA_3 treatents, and to test the effects of after-ripeing in *A. rhagadioides*.

A generalised linear model with binomial error and a probit link function was fitted to the seed longevity data (i.e. loss of viability over time), and thus fit the viability equation (Ellis and Roberts 1980);

$$v = K_i - (p/\sigma)$$

where v was the viability after p months in aging, σ is the standard deviation of the normal distribution of seed deaths in time, and K_i is the initial seed viability. An estimate of the time taken for seed viability to fall to 50% (P50) was calculated by solving for p when v = 50%. The Pearson test, Shapiro-Wilk tests, ANOVAs and GLMs were all conducted in R (R Core Team 2018).

2.4 RESULTS

The heaviest seeds had the longest germination times, hence there was a positive correlation between seed mas and t_{50} (Fig 2.3; P = 0.034), albeit based on only six species with germination data. However, there was no correlation between seed mass and longevity (P50: R = 0.44, P = 0.28), between seed mass and seed fill (R = 0.23, P = 0.59), or between embryo type and t_{50} (R = -0.41, P = 0.42).

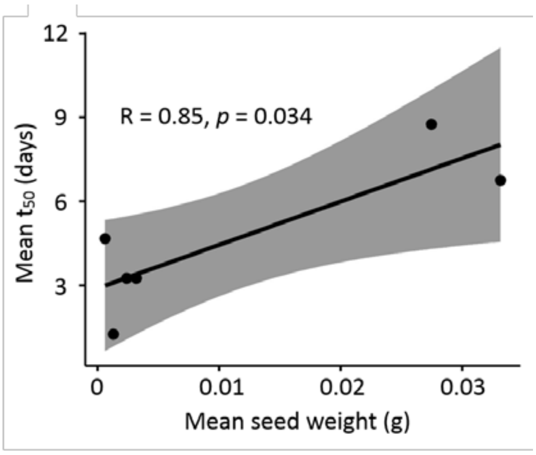

Fig 2.3: Pearson correlation between mean seed weight and mean t50.

2.4.1 Viability and dormancy

Each species in the study showed high germination in at least one diurnal temperature treatment within two weeks and without pre-treatment, except for *A. rhagodioides* and *G. parviflora*. No germination was observed for *G. parviflora* at any of the diurnal temperatures tested, nor through further treatments to relieve dormancy (boiling water and H_2SO_4 soaks, GA_3, after-ripening and the move-along method). Hence the dormancy characteristics of *G. parviflora* were not determined, and no further germination results for this species will be presented. Seed fill was high for all species, except *M. platycarpum*, which was also excluded from germination studies due to lack of viable seeds. Imbibition studies demonstrated that seeds of all species readily take up water within 72 hours of wetting (Table 2.1).

Table 2.1: Measured seed traits of species in this study.

Species	Lifeform	Age	Dry mass (g)	SF (%)	V (%)	ET	E:S	I72 (%)	DT
Atriplex rhagodioides	Shrub	12	0.06 (0.001)	94 (0.6)	67 (1.1)	Peripheral	>1	21 (1.4)	PD
Maireana. sedifolia	Shrub	2	0.13 (0.001)	97 (0.3)	93 (0.5)	Peripheral	>1	30 (2.5)	ND
Maireana pyramidata	Shrub	8	0.24 (0.005)	89 (0.9)	62 (0.9)	Peripheral	>1	16 (0.4)	ND
Casuarina pauper	Tree	5	0.32 (0.007)	72 (0.9)	35 (0.6)	Investing	~1	10 (0.6)	ND
Hakea tephrosperma	Tree	16	3.31 (0.058)	96 (0.8)	96 (0.6)	Investing	~1	91 (1.8)	ND
Alectryon oleifolius	Tree	15	2.75 (0.111)	68 (0.8)	48 (1.2)	Bent	~1	87 (3.4)	ND
Geijera parviflora	Tree	2	2.95 (0.136)	94 (0.5)	88 (1.1)	Spatulate	0.89	29 (0.7)	PD
Myoporum platycarpum	Tree	0.5	0.26 (0.005)	20 (0.7)	13 (0.6)	Straight	~1	N/A	ND

Age = age (months) of seed used in tests; Dry mass = mean weight of 100 seeds; SF = initial seed fill; V = seed viability; ET = embryo type, classified according to Martin (Martin 1946); E:S = embryo to shoot ratio (seeds without endosperm indicated as ~1 and seeds with embryo longer than seed indicated as >1); I72 = seed mass increase at 72hr; and DT = dormancy type classified according to Baskin and Baskin (2014: ND = non dormant, PD = physiological dormancy). The standard errors of means are shown in parentheses.

2.4.2 Effect of temperature on seed germination proportions

Temperature had no significant effect on maximum germination for *C. pauper*, *M. sedifolia* and *A. oleifolius* ($P \geq 0.2$ across all temperatures). However, maximum germination was significantly lower at the warmest diurnal temperature of 30/20°C for *M. pyramidata* ($P = 0.01$) and to a lesser degree for *H. tephrosperma* ($P = 0.045$) and *A. rhagodioides* ($P = 0.047$; Table 2.2).

Table 2.2: Mean values for maximum germination for each species under three diurnal temperatures.

Treatments	*Atriplex rhagodioides*	*Maireana sedifolia*	*Maireana pyramidata*	*Casuarina pauper*	*Hakea tephrosperma*	*Alectryon oleifolius*
Diurnal temp						
30/20	50.8 (6.8)^{a}	95.7 (3.7)^{a}	66.7 (2.7)^{a}	94.3 (5.5)^{a}	92.7 (2)^{a}	80 (7.7)^{a}
25/15	69.2 (2.9)^{b}	100 (1.1)^{a}	86.7 (4.7)^{b}	100 (9.8)^{a}	100 (1.7)^{b}	76.7 (11.4)^{a}
17/7	60 (2.9)^{ab}	97.8 (2.7)^{a}	88.3 (4.2)^{b}	77.1 (9.8)^{a}	100 (1.7)^{b}	66.7 (5.4)^{a}
GA$_3$						
30/20	86.2 (6.6)**	98.9 (1.8)$^{n.s.}$	63.3 (4.3)$^{n.s.}$	97.1 (7.4)$^{n.s.}$	96.9 (2)$^{n.s.}$	86.7 (8.6)$^{n.s.}$
After ripening						
30/20	94.9 (4.9)**					
25/15	93.5 (6.2)*					
17/7	98.9 (3.6)***					
GA$_3$ + after ripening						
30/20	93.5 (2.3)$^{n.s.}$					

Maximum germination is also shown for the GA$_3$ treatment (when diurnal temperature is 30/20°C), and after the after-ripening treatment for *A. rhagodioides*. Letters indicate the results of Tukey pairwise comparisons among the three diurnal temperature treatments. Treatments that share a letter are not significantly different from each other. For the GA$_3$ and after-ripening treatments, asterisks represent significant differences compared to the control treatment. For the 'GA$_3$ + after-ripening' treatment, the comparison is to the GA$_3$ only treatment (n.s. = not significant; * $0.05 > p > 0.01$; ** $0.01 > p > 0.001$; $p < 0.001$).

2.4.3 Effect of temperature on seed germination rates

Non-dormant species germinated (t_{min}) rapidly and within six days in at least one diurnal temperature treatment (Fig 2.4). The two *Maireana* shrubs reached maximum germination quickest, within one to five days, while tree species were slower to germinate. Time to maximum germination (t_{max}) was significantly affected by temperature for all species except for *C. pauper*, with a general trend of decreasing germination times as diurnal temperatures increased (Table 2.2). t_{max} was significantly longer in *M. pyramidata* and *A. oleifolius* at 17/7°C and 25/15°C than at 30/20°C ($P \leq 0.014$). The species with germination times least affected by temperatures were *H. tephrosperma* which had significantly delayed germination only at the coldest temperature (17/7°C; $P = 0.014$), and *C. pauper,* which had no significant change in germination times across all temperatures ($P = 0.25$).

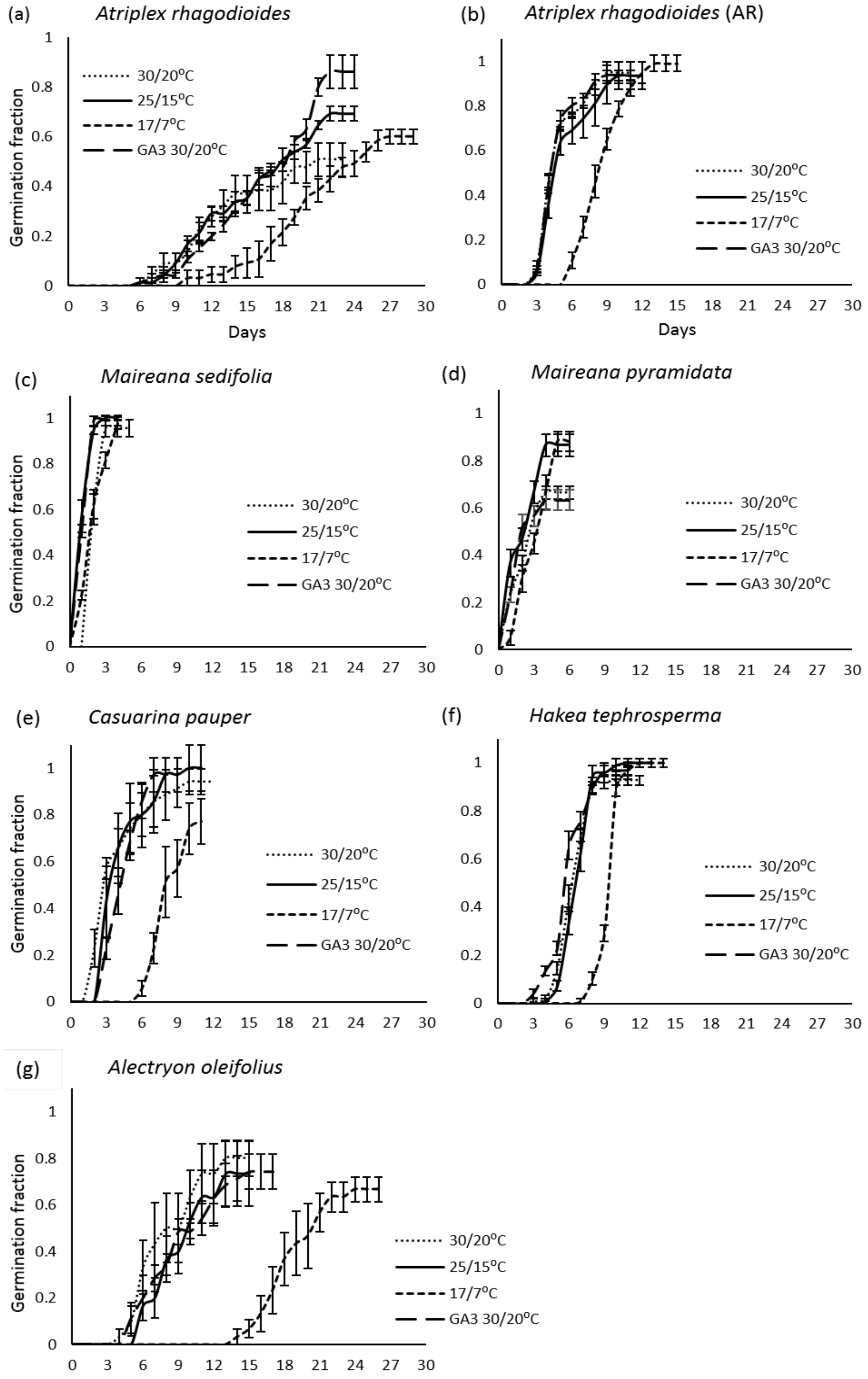

Fig 2.4: Cumulative germination (mean ± SE) across diurnal temperatures. Seeds were incubated at 30/20°C, 25/15°C and 17/7°C for 30 days. Data also includes results from seeds incubated at 30/20°C, with the addition of a growth stimulant (GA_3).

2.4.4 Germination responses to GA_3 and after-ripening

The only species with a positive germination response to GA_3 treatments was *A. rhagodioides* ($P = 0.010$; $P > 0.5$ for all other species). *A. rhagodioides* achieved t_{max} in nine days with after-ripened seed compared to twenty days with fresh seed (Fig 2.4b; Table 2.3). Similarly, for *A. rhagodioides* maximum germination of after-ripened seed was significantly higher than for fresh seed ($P \leq 0.04$ for all temperatures), and it eliminated the effect of GA_3 treatments ($P = 0.36$) and widened temperature ranges for maximum germination, indicating dormancy loss.

Table 2.3: Time to minimum, 50% and maximum germination of seeds incubated at 30/20°C, 25/15°C and 17/7°C (± standard error). *Atriplex rhagodioides* (AR) refer to seeds rendered non-dormant through a 12 month after-ripening.

	Mean t_{min}			**Mean t_{50}**			**Mean t_{max}**		
Species	17/7°C	25/15°C	30/20°C	17/7°C	25/15°C	30/20°C	17/7°C	25/15°C	30/20°C
Alectryon oleifolius	16.0 (0.9)	6.5 (0.5)	5.6 (0.5)	20.3 (0.9)	12.3 (2.7)	8.8 (1.7)	21.8 (1.0)	14.8 (1.8)	10.3 (1.3)
Casuarina pauper	6.5 (0.3)	3.3 (0.3)	2.0 (0.0)	9.0 (0.6)	4.5 (1.2)	3.3 (0.3)	9.8 (0.6)	7.5 (1.0)	7.5 (1.04)
Hakea tephrosperma	7.8 (0.3)	4.8 (0.3)	4.3 (0.5)	10.0 (0.0)	7.3 (0.3)	6.8 (0.3)	11.3 (0.3)	9.3 (0.8)	8.5 (0.5)
Atriplex rhagodioides	14.0 (1.8)	8.3 (0.9)	7.8 (0.9)	24.8 (1.0)	18.5 (1.0)	16.5 (1.8)	26.0 (0.4)	21.8 (0.3)	20.0 (0.6)
Atriplex rhagodioides (AR)	6.0 (0.0)	3.0 (0.0)	3.0 (0.0)	8.7 (0.3)	5.0 (0.0)	4.7 (0.3)	12.7 (0.3)	9.7 (0.3)	9.0 (0.0)
Maireana pyramidata	1.5 (0.3)	1.0 (0.0)	1.0 (0.0)	3.8 (0.3)	2.5 (0.29)	3.3 (0.3)	5.0 (0.0)	4.0 (0.0)	3.5 (0.3)
Maireana. sedifolia	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	2.3 (0.3)	1.3 (0.3)	1.3 (0.3)	4.0 (0.0)	2.8 (0.3)	2.0 (0.0)

2.4.5 Seed longevity

Myoporum platycarpum was the only species to exhibit characteristics of recalcitrant seeds, meaning they do not survive desiccation or aging. Seeds of *M. platycarpum* were freshly collected and most had no embryo, and of the few that had an embryo most were non-viable. Seed freshly picked from adult trees showed only 13% viability, which fell to half that within one month of aging, and was close to 0% viability within six months of aging (Fig 2.5). Most species showed a substantial decline in viability (>50%) within 12 months of aging, with the exception of *H. tephrosperma*, *A. rhagodioides* and *C. pauper*. These three species experienced less than 20% decline in viability within 12 months. The only species to show a decline in seed viability of <10% during 24 months of aging was *H. tephrosperma*. Seed longevity, or P50, for each species was (in order of longest to shortest lived, in months): *H. tephrosperma*, 84.1; *A. rhagodioides*, 32.0; *C. pauper*, 19.7; *M. sedifolia*, 14.7; *M. pyramidata*, 11.5; *G. parviflora*, 10.7; *A. oleifolius*, 8.7; *M. platycarpum*, 3.0.

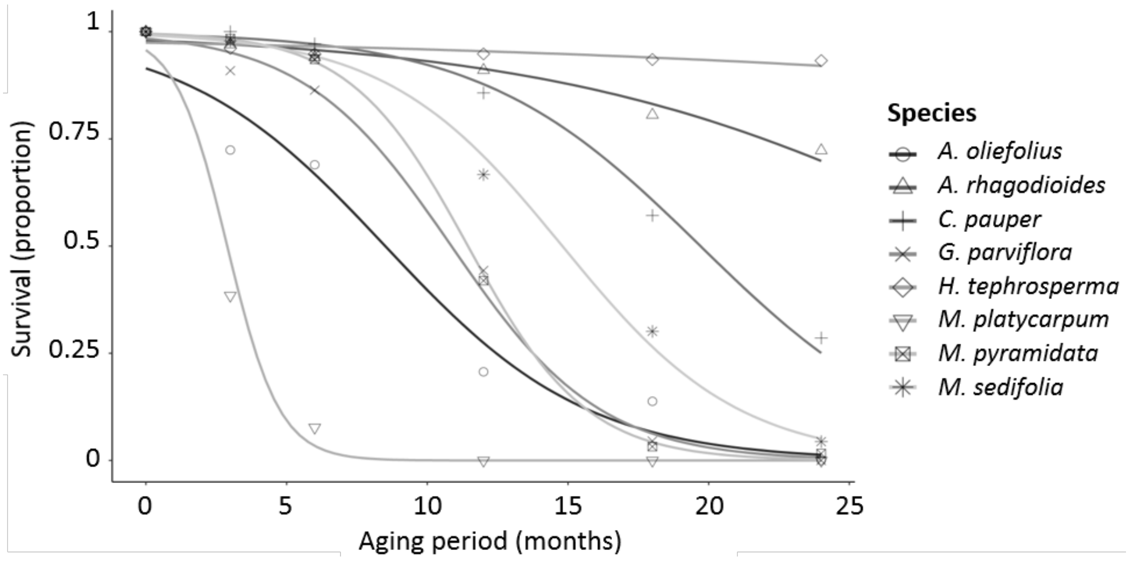

Fig 2.5: Loss of seed viability with aging. Seed age at beginning of experiment are show in Table 2.1.

2.5 DISCUSSION

Arid species in this study were generally categorised by two types of adaptive strategies to facilitate seed germination in sporadic rainfall: 1) rapid germination across a wide range of diurnal temperatures, or 2) dormancy and/or long-lived seeds to temporarily delay, or stagger, germination. Our study demonstrates that rapid germination is a common, alternative and important strategy in seeds from arid zone species, which allows seeds to capitalise on sporadic rainfall. Seeds of three species (*M. pyramidata*, *A. rhagodioides* and *H. tephrosperma*) had significantly higher germination at cooler temperatures, than at 30/20°C, hence avoid germination when evaporation rates are highest (Environdata 2019). Germination inhibition at hottest temperatures is considered an important germination strategy for seeds with dormancy or longevity in this study. We also demonstrated the tendency for seed weight and embryo type to be correlated to germination rate of the species in our study. Conversely, seed mass was unrelated to longevity and seed fill. We recommend further seed-mass germination studies, using a greater suite of indigenous species from similar bioregions, to better understand the role of seed morphology in prescribing germination behaviour.

2.5.1 Rapid germination across wide diurnal temperatures

All non-dormant seeds of species in this study exhibited rapid germination rates, which suggests that rapid germination is particularly well suited to this environment and may be at a selective advantage over other seed germination strategies. For temperate species, seeds that germinate in less than four days are considered to have rapid germination (Grime et al. 1981) although, for annual species, rapid germination means germinating within 24 hours (Gutterman 2001). Considering all species in this study are slow-growing, perennial, woody species, we herein refer to rapid germination as species that germinate (t_{min}) within 4 - 6 days. All species, except for dormant seeds of *G. parviflora* and *A. rhagodioides*, commenced germination within six days upon wetting and displayed 50% germination in ≤9 days at the highest temperatures tested. Rapid germinating species are able to take advantage of single rainfall events, whereas slow germinators require several rainfall events persisting across days (Jurado and Westoby 1992), which rarely occurs in the arid zone studied here (Environdata 2019). All species achieved >50% germination across all temperatures tested, suggesting they have wide thermal ranges for germination. Wide thermal ranges for germination allow seeds to take advantage of stochastic rainfall events that occur during any season. While this may enable opportunistic plant recruitment, additional studies should quantify hydrothermal niches for seed germination to further understand recruitment timing across different seasons.

Germination strategies, particularly those that affect the timing of germination such as dormancy, may be important determinants of population dynamics in arid ecosystems. For example, vegetation classification in this arid zone prior to disturbance was Belah-Rosewood Woodland and Belah-Bluebush Woodland (Ogyris 2000), of which the dominant species include the non-dormant, fast germinators *C. pauper* and *Maireana* shrubs. The two species that have seeds with physiological dormancy, *A. rhagodioides* and *G. parviflora*, and non-dormant seeds of *A. oleifolius*, had the slowest germination speeds, are less dominant (Read 1987) and appear as scattered individuals throughout the landscape (Ogyris 2000). Although the age of seeds in this study varied and pre-storage components may have contributed to aging, longevity or dormancy loss in some species, reports of non-dormancy here are consistent with the findings of Callister (Callister 2004) for all species, except *M. platycarpum*. Further studies are required to confirm dormancy in fresh seeds of *C. pauper*, *H. tephrosperma* and *A. oleifolius*. The lack of seeding events in these species during this study (potentially due to drought conditions) suggests that acquiring the quantities of seed required for their restoration may become more challenging under climate change.

Rapid germination appears to be unrelated to other morphological seed traits, except for seed mass and embryo type. All seeds in this study had fully developed embryos without an endosperm, or with embryos that are coiled and larger than the seed, and these are traits that are generally thought to indicate a rapid germination strategy (Vandelook et al. 2012; Vivrette 1995). Germination for seeds with peripheral embryos (including *Atriplex* and *Maireana*) is typically very fast because it involves merely the uncoiling of the spiral embryo upon imbibition, which ruptures the seed coat (Wallace et al. 1968). Many such species with peripheral embryos inhabit high-stress environments, where the rapid exploitation of temporarily favourable conditions for germination is more important (Parsons 2012). Our results showed that the size and development of embryos was not a consistent predictor of germination strategy.

The species in this study with the fastest germination rates (*C. pauper*, *M. sedifolia* and *M. pyramidata*), are dominant species from the region, and produced small seeds that were easier to obtain due to frequent and prolific seeding events. High seed production requires high maternal input but the risk of population crashes are mediated because these species are less dependent on high seed survival rates (Larson and Funk 2016). Other studies report strong evidence for survival advantages associated with larger seeds under stressful conditions (Bergholz et al. 2015; Lebrija-Trejos et al. 2016; Leishman and Westoby 1994) but, considering the variable size of arid seeds and the trade-off associated to increased seed production in small seeded species, survival advantages of large-seeded species does not appear large enough to counterbalance the advantage of small-seeded species during seed production (Moles et al. 2000; Moles and Westoby 2004; Moles 2018). We found that small seeded species were amongst the fastest to germinate, however the negative relationship between germination speed and seed size was weak, suggesting that seed size may not always be a reliable proxy for germination rate. Future studies are required to test a larger number of species of a greater order of magnitude of seed mass variation, prior to making general assumptions about the relationship between seed mass, germination rate and success.

While the germination responses of *M. platycarpum* were not classified in this study, Callister (Callister 2004) shows that it germinates to 50% within 4-5 days following wetting, consistent with other non-dormant trees species in this study. Callister et al. (2018) suggests that seed-dormancy, not seed viability, is the key factor limiting germination in *M. platycarpum.* In contrast, as observed in our study, examining embryo firmness and colour through dissection microscopy is not an appropriate method to assess seed viability in *M. platycarpum* because TZ results show that healthy looking embryo are often dead (Fig 2.2f). Alternative viability testing, by assessing seed metabolic rate, may provide more accurate viability assessment (e.g.; Dalziell and Tomlinson 2017) and should be considered for future testing. Our results suggest that seeds of *M. platycarpum* are non-dormant and that seed viability and short-lived seeds are the key factors inhibiting germination.

2.5.2 Low prevalence of seed dormancy

Most seeds of plants from the arid zone have dormancy traits that enable germination to coincide with periods of highest water availability (Baskin and Baskin 2014; Bell 1999), yet only two species in this study (*A. rhagodioides* and *G. parviflora*) showed dormancy traits. These two species presented physiological dormancy traits as they readily imbibe water and have fully developed embryos, but failed to germinate to maximum potential within thirty days without treatment (Baskin and Baskin 2014). *A. rhagodioides* also showed a positive response to GA_3 before after-ripening. The dormancy cues of *G. parviflora* remain unresolved as all treatments failed to relieve dormancy, and there was a lack of viable seed available for further germination treatments. Most species from the same family as *G. parviflora*, the Rutaceae family, produce seeds with physiological dormancy and are commonly associated with complex germination requirements (Auld 2001; Baskin and Baskin 2014; Martyn et al. 2009; Ooi 2007). Fewer species showed signs of dormancy than was expected. There is potential that due to the age of seeds used for this study, some of the study species may have exhibited dormancy traits as fresh seed. We have classified four such species (*A. oleifolius*, *C. pauper*, *H. tephrosperma* and *M. pyramidata*) as non-dormant, and we do not believe there would be significant levels of dormancy in the fresh seed of these species. Callister (Callister 2004) provides supporting evidence for this assertion for *C. pauper* and *A. oleifolius.* Local nurseries (including The Seeds of South Australia Database) and seed practitioners also support the claims of non-dormancy in these species (I. Sluiter, A. Quamby, T. Langdon, pers. comm. 2018), and there is evidence of non-dormancy in congeneric species within the genus (Baskin and Baskin 2014). Traits that increase the likelihood of germination coinciding with periods of highest water availability may be less important in environments with unpredictable wetting pulses.

Delayed germination through dormancy has been observed in many arid zone species (e.g.; Commander et al. 2017; Gremer et al. 2016; Lewandrowski et al. 2018). Similarly, for *A. rhagodioides,* a small proportion of seeds germinate upon maturity, or upon seed dispersal, but germination rate and proportion improve as seeds age. This suggests that seeds can remain in the soil or canopy for years and stagger germination across seasons, which spreads the risk of recruitment failure through time and increases the probably that favourable conditions for seedling establishment will occur during the lifespan of a seed cohort (Fan et al. 2018b; Gremer et al. 2016). Physiological dormancy in *A. rhagodioides* was relieved through a period of after-ripening, a trait also reported in other *Atriplex* species (Meyer et al. 1998; Meyer 2008). After-ripening also enables a wider temporal window for germination which suggests that germination opportunities increase as seeds after-ripen. Developing a short-term soil seedbank, before the onset of suitable rainfall events, is an important adaptation in response to the unpredictability of resource availability in arid ecosystems. However, *A. rhagodioides* and *G. parviflora* were the only dormant species in this study, and non-dormant and prolifically-seeding trees are the most dominant species of the region (Sluiter and Sluiter 2015). This again suggests that in arid zones without distinct wet seasons, playing it safe through dormancy may be less important than previously assumed.

The literature on bet-hedging predominately investigates annual species with short life-cycles (i.e.; Gremer and Venable 2014; Venable 2007), whereas this study focuses on long-lived perennial species. Bet-hedging is more likely in annuals because the consequences of death of entire seed cohorts are greater (Gremer and Venable 2014; Venable 2007). Comparative studies indicate that seed dormancy is higher in annuals than in perennials (de Waal et al. 2016; Rees 1993; Thompson et al. 1998), although very few studies investigate bet-hedging in perennial shrubs (Letnic et al. 2000; Thompson et al. 1998), and no such studies exist for arid tree species. Perennial species (including *C. pauper*, *M. platycarpum* and *M. sedifolia*) can have many flowering and seeding events throughout their lifespan. Thus, losing an entire seed cohort is of little consequence, reducing the selection pressure to maintain a soil seedbank (Auld 1995; Wotton 1993). Additionally, *C. pauper* (Murdoch 2005), *H. tephrosperma* (Murdoch 2005), *M. platycarpum* (Chesterfield and Parsons 1985) and *A. oliefolius* (Govt of SA 2010) have the capacity to regenerate via root suckers, which may further mediate the impact of losing entire seed cohorts for consecutive years, and possibly negate the need for dormancy. Our study supports the notion that perenniality selects against seed dormancy (de Waal et al. 2016; Rees 1994; Tuljapurkar 1990) however, we only tested dormancy in eight species and studies from other arid zones report dormancy in many perennial species that seed frequently. Therefore, we recommend further research testing the prevalence of dormancy for long-lived species that fruit prolifically.

The ability to delay seed release, through serotiny, may further mediate the likelihood of dormancy and bet-hedging in *H. tephrosperma* that has non-dormant seeds with exceptional seed longevity. Through delayed seed release, seeds of *H. tephrosperma* can likely persist is the canopy for many years following seed maturity, as reported in congeneric *Hakea* species (Groom and Lamont 1997). Serotiny levels in *H. tephrosperma* have not been investigated to-date, although only one occurrence of seed release was observed in populations from the study site during the three years of this study (personal observation). However, the level of serotiny in *Hakea* is positively related to follicle mass (Groom and Lamont 1997), and hence the large and woody follicles of *H. tephrosperma* suggest it is strongly serotinous. While serotiny in Proteaceae is considered beneficial to surviving in fire-prone landscapes, it is also observed in fire-free landscapes (Bradshaw et al. 2011) or, like this study site, where small bushfires occur at interdecadal scales. We suggest that seed release in *H. tephrosperma* is triggered by seasonal temperatures and/or humidity, rather than fire, and is a crucial survival strategy for this species because it is non-dormant and flowers infrequently when rainfall is limited.

Low serotiny and bet-hedging (with the exception of *H. tephrosperma* and *A. rhagodioides*) in species in this study suggest a strong selection for rapid flowering and seed dispersal in response to rainfall. For example, the two *Maireana* species in this study can flower at any time of the year, but usually do so following large rain events (Hall et al. 1964; Wotton 1993). Furthermore, their seeds are encircled by a papery wing—a trait adapted for dispersal away from the adult plant by wind soon after it has matured, or when dehiscing. The two non-dormant tree species (*C. pauper* and *M. platycarpum*) also flower prolifically, have seeds that are rapidly dispersed by wind, and have no apparent adaptations for serotiny or seed banking. Conversely, fruiting in *A. rhagodioides* and *H. tephrosperma* may not occur every year, but they have the capacity to recharge their seed bank through flowering and fruiting during favourable periods. Thus, because dispersal ability, serotiny and bet-hedging all function to avoid the risk of seedling emergence during unfavourable conditions, they may substitute for one another so that selection for one may weaken selection for the other strategy (Klinkhamer et al. 1987; Siewert and Tielbörger 2010; Snyder 2006). For species that fruit irregularly with no obvious adaptations for delaying seed release and germination (*A. oliefolius* and *G. parviflora*), there will be limited recruitment opportunities with increasing aridity and rainfall variability. As such, we have concerns for the persistence of these species under climate change.

Seed longevity is an alternative strategy to spread the risk of reproductive failure across time, and may further reduce the requirement for dormancy and bet-hedging (Rees 1993; Tuljapurkar 1990). Seed longevity is also critical for species with dormancy traits, or serotinous species with canopy-stored seed, because seeds may need to survive multiple seasons. Our results are consistent with other studies that have found serotinous species typically have orthodox seeds that are long-lived (Merritt et al. 2014), or tolerant to desiccation. However, longevity results in this study may only reflect seed-aging behaviour during *ex situ* storage and further studies should test seed persistence *in situ* to understand soil-seed banking dynamics. Species from arid environments are more likely to have comparatively long-lived seeds than those from cooler, wetter ecosystems (Probert et al. 2009). Nonetheless, most species in this study had significantly higher longevity than expected (Merritt 2014; Merritt et al. 2014; Probert et al. 2009) and we suggest that high seed longevity is a key adaptation to cope with the unpredictability of rainfall at the study site. Perennial plants that invest in seed longevity as a survival strategy increase their probability of encountering conditions favorable for seedling establishment (Ehrlén and Van Groenendael 1998; Zeineddine and Jansen 2009), and our results support the notion that longevity can negate the need for dormancy. In summary, a perennial life history and long-lived seed together reduce the likelihood of bet-hedging for the species in this system, where dominant perennial plants appear to invest less in seed dormancy and bet-hedging, and instead select for seed longevity and increases to offspring numbers.

2.6 CONCLUSION

We discuss seed morphology and physiology, and the germination behaviour of seeds that may facilitate seed survival and growth in arid zones. Most species exhibit rapid germination across wide diurnal temperatures, often producing prolific quantities of seed, which enables species to take advantage of rainfall events that fall across all seasons. Fewer species tend to avoid unfavourable conditions by delaying germination through seed dormancy and possibly bet-hedging. High seed longevity under *ex situ* aging was observed in most species included in this study. While seed dormancy is an important survival strategy for an arid seed, rapid germination and high seed production rates may be alternative regeneration traits and have a crucial role in explaining population dynamics in arid ecosystems with unpredictable rainfall. In such systems, the benefits of rapid germination may outweigh those associated with delayed germination through dormancy, and the population structure of remnant ecosystems in the region (which are dominated by rapid germinators) may be a testament to this.

2.7 ACKNOWLEDGEMENTS

We wish to acknowledge the environmental team at Tronox Mining for instrumental support and access to land and to Kings Park Science for trainings in seed-based technologies. Finally we thank Dr Ian Sluiter and Tim Zwiersen for sharing insights to seed-based restoration approaches in arid zones and support for the project.

CHAPTER 3

The risk-takers and avoiders: germination sensitivity to water stress in an arid zone with unpredictable rainfall

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3.1 ABSTRACT

Water availability is a critical driver of population dynamics in arid zones, and plant recruitment is typically episodic in response to rainfall. Understanding species' germination thresholds is key for conservation and restoration initiatives. Thus, we investigated the role of water availability in the germination traits of keystone species in an arid ecosystem with stochastic rainfall. We measured seed germination responses of five arid species, along gradients of temperature and water potential under controlled laboratory conditions. We then identified the cardinal temperatures and base water potentials for seed germination, and applied the hydrotime model to assess germination responses to water stress. Optimum temperatures for germination ranged from 15°C – 31°C under saturated conditions (0 MPa), and three species had low minimum temperatures for germination (< 3°C). A small proportion of seeds of all species germinated under dry conditions ($\Psi \leq -1$ MPa), although base water potential for germination (Ψ_b50) ranged from -0.61 MPa and -0.79 MPa. Species adhered to one of two germination traits: (1) the risk-takers which require less moisture availability for germination, and which can germinate over a wider range of temperatures irrespective of water availability (*Casuarina pauper* and *Maireana pyramidata*), and (2) the risk-avoiders that have greater moisture requirements, a preference for cold climate germination, and narrower temperature ranges for germination when water availability is low (*Atriplex rhagodioides*, *Maireana sedifolia* and *Hakea leucoptera).* High seed longevity under physiological stress in *H. leucoptera*, combined with a risk-avoiding strategy, allows bet-hedging. The hydrotime model predicted lower base water potentials for germination than observed by the data, further supporting our assertion that these species have particular adaptations to avoid germination during drought. This study provides insights into the complex physiological responses of seeds to environmental stress, and relates seed germination traits to community dynamics and restoration in arid zones.

3.2 INTRODUCTION

Arid plant recruitment is infrequent and episodic due to water limitation (Schwinning and Sala 2004; Wiegand et al. 2004). Understanding the determinants of recruitment losses is crucial for the restoration of ecosystems affected by changes to land-use and climate (Commander et al. 2019). Seed germination is a critical life transition stage for arid plants and is largely controlled by water availability (Adams 1999), hence moisture conditions must coincide with appropriate germination traits (Clauss and Venable 2000; Köchy and Tielbörger 2007). Some arid plant species adopt a risk-taking strategy, and produce seeds with low moisture thresholds that germinate in response to small rainfall events (Ramírez-Tobías et al. 2014), while others adopt a risk-averse strategy so germination occurs only in wet soils (Merino-Martín et al. 2017; Mollard and Naeth 2015; Sfairi et al. 2012). As such, small rainfall events may only affect species with a risk-taking strategy and fast response times, while larger rainfall events are required to effect the growth and establishment of risk-avoiders – generally higher vascular plants and slow-growing species, including tree species (Noy-Meir 1973; Schwinning and Sala 2004). We assume that seed germination in arid zones occurs mostly in response to large rainfall events (Gutterman 1994), yet species responses to different-sized rainfall events are rarely quantified (but see Meyer and Allen 2009), even though they ultimately determine community dynamics in arid zones (Reynolds et al. 2004).

The emergence of germinated seed appears to be the major recruitment bottleneck for many arid species (Chambers 2000; James et al. 2011; Pyke 1990). Moisture availability in arid zones is driven by rainfall, and is a crucial determinant of germination, seedling growth and the distribution patterns of species (Gutterman 1993). Generally both germination rate and germination proportion decrease progressively with decreasing soil water potential (Bradford 1990). As ambient temperatures increase, so does evaporation and evapotranspiration (Feng et al. 2014b), and the temporal period of moisture availability is decreased (Wang et al. 2012). Seeds that germinate when moisture is available for short periods face the risk of emerging during conditions unfavourable for seedling establishment (Gremer and Venable 2014). Some arid species show particular adaptive germination mechanisms to restrict germination to wetter periods (Zeng et al. 2010) or to avoid germination during summer temperatures (Sánchez et al. 2014). However, physiological thresholds for germination in a range of native species from within the same climatic origin are rarely assessed (Flores et al. 2017; Hu et al. 2015; Köchy and Tielbörger 2007) as most studies focus on temperature dynamics only (e.g.; Lai et al. 2016). Defining thresholds for germination has proven useful for crop and weed emergence models (Dürr et al. 2001; Forcella et al. 2000; Gardarin et al. 2012), however it has not been widely applied to understand recruitment and survival in native species from unpredictable environments. When species response thresholds are empirically tested and quantified, there is potential to predict community structure under climate change and specific management techniques (James et al. 2013).

Physical traits of seeds, and adult plant traits, are often used as a proxy for germination strategy (e.g.; Hoyle et al. 2015; Moles and Westoby 2004). Large seeds may have an increased chance of seedling survival and establishment under dry conditions (Daws et al. 2008; Leishman and Westoby 1994; Moles and Westoby 2004), although small seeds tend to germinate faster than heavy seeds (Vivrette 1995), which is considered an important advantage for arid species (Chesson et al. 2004). The importance of the seed-size water-potential relationship varies among biomes (Metzner et al. 2017) and are difficult to predict under small moisture gradients (García-Baquero et al. 2015; Tielbörger and Petru 2008). Furthermore, annual plants tend to show a negative relationship between seed mass and base water potential for germination, whereas perennials display a negative relationship between base temperature for germination and seed mass (Arène et al. 2017). Hence, the link between seed size and hydrothermal thresholds to germination remain unclear and warrant further testing.

Germination is also linked to a species' ecological niche (Arène et al. 2017), and the literature suggests differences in opinion of the influence of the environment in prescribing germination niches (Fang et al. 2017; Losos 2008; Vandelook et al. 2008). Certainly, plant taxa that are often associated with dry or saline environments, such as *Atriplex*, have greater tolerance ranges to water stress than other taxa (Deng et al. 2014; Shaygan et al. 2017). The interplay between adult plant traits and climate have been widely studied (Pérez-Harguindeguy et al. 2013; Sack et al. 2013), but we lack understanding of the link between germination thresholds, climate, and seed traits (with the exception of seed size; Arène et al. 2017; Moles et al. 2007). Strong relationships exist between minimum temperatures for germination and the climatic conditions of biomes that species inhabit (Rosbakh and Poschlod 2015), and between seed size and base water potentials for germination (Arène et al. 2017; Daws et al. 2008) but, to our knowledge, no studies have explored how the unpredictability of rainfall may influence the seed traits and germination thresholds of native species.

Hydrotime models quantify the effects of water potential on seed germination and provide a useful tool to assess germination sensitivity relative to environmental conditions (Bradford 2002). These models are based on the linear increase in germination rates from base (T_b), through optimum (T_{opt}) temperatures for germination, and the steady decline in germination rate as conditions dry (Bradford 1990; Bradford 2005; Gummerson 1986). Although departures of actual seed germination from the hydrotime model are frequently reported at sub-optimal and supra-optimal temperatures (Grundy et al. 2000; Kebreab and Murdoch 1999), it can be a useful tool in defining seed responses to micro-climate conditions, and the germination niche of seeds (Bloomberg et al. 2009; Watt et al. 2011). Few studies have defined the physiological thresholds for seed germination from wild species in arid zones (Arnold et al. 2014b; Frischie et al. 2019; Hu et al. 2015; Lewandrowski et al. 2016), hence our understanding of the role of water availability in the germination strategy of native species in the arid zone is limited.

Germination triggered by small rainfall events is risky, particularly when the chance of follow-up rainfall is low, hence we predict high moisture thresholds for germination as the dominant strategy. We expect a higher proportion of seeds to germinate in cool temperatures, when moisture from rainfall events remains in soil for longer due to reduced evaporative water loss. We also expect a positive correlation between seed mass and base water potential for germination. This study provides insight into the complex germination behaviour of non-dormant, arid seeds, and relates seed germination traits to community dynamics in arid zones.

3.3 METHODS

3.3.1 Seed collection and location

Seeds were collected from arid, south-west New South Wales (33°22’05”S, 142°13’36”S), from remnant populations targeted for restoration. Vegetation at the study site is classified as Belah-Rosewood Woodland and Belah-Pearl Bluebush Woodland (Sluiter and Sluiter 2015). The tree species in these woodland communities are dominated by *Casuarina pauper* F.Muell. ex L.A.S.Johnson (Casuarinaceae), with smaller patches of *Alectryon oleifolius* ssp. *canescens* S.T.Reynolds (Sapindaceae). Other tree species that appear as scattered individuals across the landscape include *Myoporum platycarpum* ssp. *platycarpum* R.Br, *Geijera parviflora* Lindl. (Scrophulariaceae), and *Hakea* species including *H. leucoptera* ssp. *leucoptera* R.Br. and *H.*

tephrosperma R.Br. (Proteaceae). The understory is dominated by *Maireana sedifolia* (F.Muell.) Paul G.Wilson. Chenopod shrubs are common, but less prevalent, and include *M. pyramidata* (Benth.) Paul G.Wilson and *Atriplex* species, such as *A. rhagodioides* F.Muell. The five keystone arid species included in this study are found in the remnant vegetation of the region—two trees (*Casuarina pauper* and *Hakea leucoptera*), and three shrubs (*Atriplex rhagodioides*, *Maireana sedifolia* and *Maireana pyramidata*). Mean monthly rainfall at the study site is 24 mm (BOM 2018) and average annual rainfall can often fall below 200 mm for consecutive years. Temperatures range from 2°C to 47°C with cooler mean daily temperatures from May to August. Evaporation is higher than rainfall across all months (Fig 3.1) and, unlike most arid zones across the globe, there is no distinct wet season.

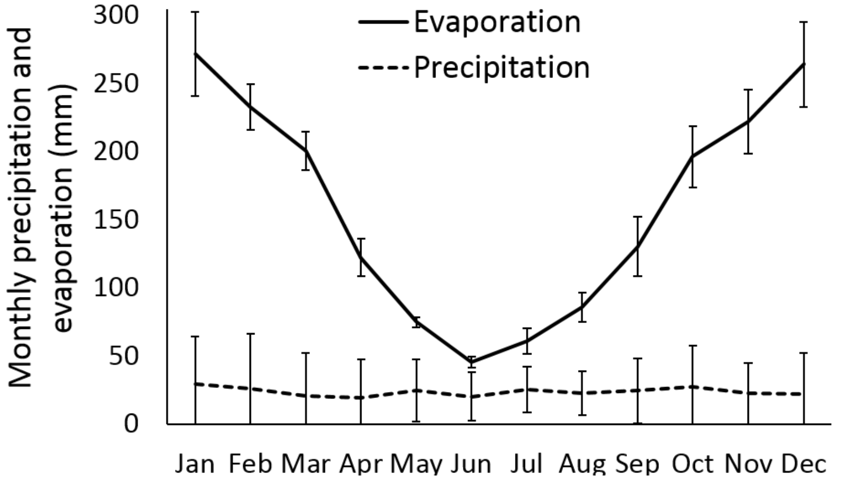

Fig 3.1: Mean monthly precipitation, from 1956-2016 (BOM 2018) and mean monthly evaporation, from 2013-2018 (Environdata 2019) at the study site. Errors bars represent standard deviation.

3.3.2 Seed collection and processing

Fresh seeds were collected for testing from within a 100-km radius of the centre of the study area. Seeds were either personally collected (C. Duncan), donated from Ecotypic Pty Ltd and Cristal Mining, or purchased from Ogyris Pty Ltd. All species included in this study were non-dormant, except for *A. rhagodioides,* which has physiological dormancy that was alleviated through after-ripening for 18 months prior to the experiment (Duncan et al. 2019). Seeds were manually cleaned and all seed covering structures, such as bracts, were removed. Seed mass was determined using the mean of three replicates of 100 seeds each, with results then adjusted to account for seed fill (determined by longitudinal cut tests) and divided by 100 to represent weight (g) per seed.

3.3.3 Germination under water and temperature regimes

Seeds were incubated under eight temperatures from 5°C – 40°C (at 5°C increments), and nine water potential treatments from saturated to wilting point (0, -0.01, -0.15, -0.25, -0.35, -0.5, -0.75, -1.0 and -1.5 MPa), applied through different Polyethylene Glycol solutions (PEG, *PEG-8000, Sigma Aldridge, Sydney, NSW, Australia*). As such, there were 72 treatment combinations in total. The PEG solutions were prepared in water and calculated according to Michel (1983). Three replicates of 30 seeds per species were used for each water potential treatment, except for two species. To overcome low seed viability (~35%) of *C. pauper*, the number of seeds per replicate for this species was increased to 40. For *H. leucoptera* the number of seeds per replicate was reduced to 25 due to low seed production and availability. Seeds were incubated in a 90-mm Petri dish on filter paper moistened with 5 ml of the relevant PEG solution and sealed tightly with cling film before, and during, incubation. To prevent microbial outbreak and ensure constant hydration during germination tests, seeds were transferred to sterilised Petri dishes weekly, on new filter papers moistened with the same appropriate PEG solutions. Seeds were incubated under alternating 12-hr light/dark schedule incubators (Lindner and May, Model: LMRIL 396, Windsor, Australia), provided by 2 x 36-Watt fluorescent globes. Prior to germination treatments, seeds of all species were surface sterilised by soaking in 1% sodium hypochlorite for one minute, then rinsed for 40 seconds with double distilled water. Seed germination (when the radicle emerged to at least half of seed size) was recorded every second day. Germination was scored for 30 days, or until germination ceased for four consecutive readings across all treatments. Incubator temperature was monitored every two days and the experiment was repeated when the temperature fluctuated 2°C or more for two consecutive readings.

Seed viability was assessed by dissecting seeds after staining in a 1% solution of 2,3,5-triphenyl tetrazolium chloride (TZ), except for *H. leucoptera* which was germinated on filter paper at warm diurnal temperatures due to consistently poor TZ stain results and a germination response of 100%. Embryos that completely absorbed the TZ stain were scored as viable, and embryos that only partially absorbed the TZ stain were recorded as non-viable seeds. Seed viability was assessed within two days prior to the experiment and final germination proportion was corrected for viability and calculated using the following equation (Sweedman and Merritt 2006):

$$VAG = \frac{Final\ germination\ (\%)}{Mean\ viability\ (\%)} \times 100$$

The effects of temperature and water stress on embryo health were assessed by performing further seed viability tests at the end of the experiment, by dissecting and staining seeds using the TZ methods mentioned above.

3.3.4 Calculation of cardinal temperatures

The time to 50% germination (t_{50}) was determined by fitting a sigmoid curve to the mean values of germination proportion over time for each species, at each water potential. The sigmoid model describes the cumulative germination proportion (G) over time (t) and is described by:

$$\mathrm{G} = \frac{\mathrm{G_{max}}}{1 + e^{-a(t-b)}}$$

where G_{max} is the maximum germination percentage, t is the time required for specific germination fractions, and *a* and *b* are constants. Estimates of cardinal temperatures were calculated using germination rate (GR = 1/t) at 0 MPa, plotted against temperature. We used the segmented package in R (Muggeo 2008; R Core Team 2018), which used iterations to fit a two-piece segmented linear model to the data for germination rate over time. From the two linear regressions in each segmented model, the intercepts with the temperature axis provided estimates for T_b and T_c, respectively, and T_{opt} is the temperature at which the two linear regressions intercept (e.g. Frischie et al. 2019). Temperatures from the base (T_b) to optimum (T_{opt}) were species sub-optimal temperatures for germination. Temperatures from T_{opt} to ceiling (T_c), or maximum temperatures, where germination rate decreases, were species supra-optimal temperatures for germination. In species with rapid germination rates (*M. sedifolia* and *M. pyramidata*), the supra-optimal temperature range was exceptionally and atypically small, and the experiment did not capture the decrease in germination rate above T_{opt}, such that the germination rate at the next 5°C increment was 0. In these cases, the first temperature after T_{opt} provided an estimate of T_c, though we acknowledge the actual value of T_c will be in the small temperature range between T_{opt} and our estimate of T_c.

3.3.5 Modelling base water potentials for germination

To determine the base water potential for 50% germination (Ψ_b50), we created a linear model to describe germination proportion at different water potentials using the experimental data. From this relationship, we solved for the water potential at 50% germination. We then compared Ψ_b50 at each temperature to parameters generated by the hydrotime model which uses the following probit regression analysis (Dahal and Bradford 1990):

$$Probit(g) = [\Psi - (\theta H / t_g) - \Psi_b(50)] / \sigma\Psi_b$$

where Ψ is the seed water potential, θ_H (MPa h^{-1}) is the hydrotime constant, t_g is the germination time (h) of the corresponding germination fraction, $\Psi_b(50)$ is the base or threshold water potential required to achieve 50 % germination of the seedlot, and $\sigma\Psi_{b\ is}$ the standard deviation. Calculation of hydrotime parameters was performed using the population-based threshold model spreadsheet, developed by UC Davis Department of Plant Science. Correlations between seed weight and Ψ_b50 were assessed using a linear model in R (R Core Team 2018).

3.4 RESULTS

3.4.1 Germination proportion effected by temperature and water potential

Under saturated conditions (0 MPa), all species germinated within the 30-day experiment when temperatures were 10°C–30°C (Fig 3.2). No germination occurred at 40°C for any species, while *H. leucoptera* and *M. sedifolia* also showed no germination at 35°C. The only two species that failed to germinate at the lowest temperature tested (5°C) were *C. pauper* and *M. pyramidata*. These were also the only two species to germinate to 50% at 35°C. While temperature envelopes for germination were wide under saturated conditions (0 MPa), they were much narrower at dry conditions, particularly for *A. rhagodioides*, *M. sedifolia* and *H. leucoptera* (Fig 3.2). At water potentials ≤ -0.75 MPa, no germination occurred at temperatures > 30°C for *A. rhagodioides* and *M. sedifolia*, and at temperatures ≥ 25°C for *H. leucoptera*.

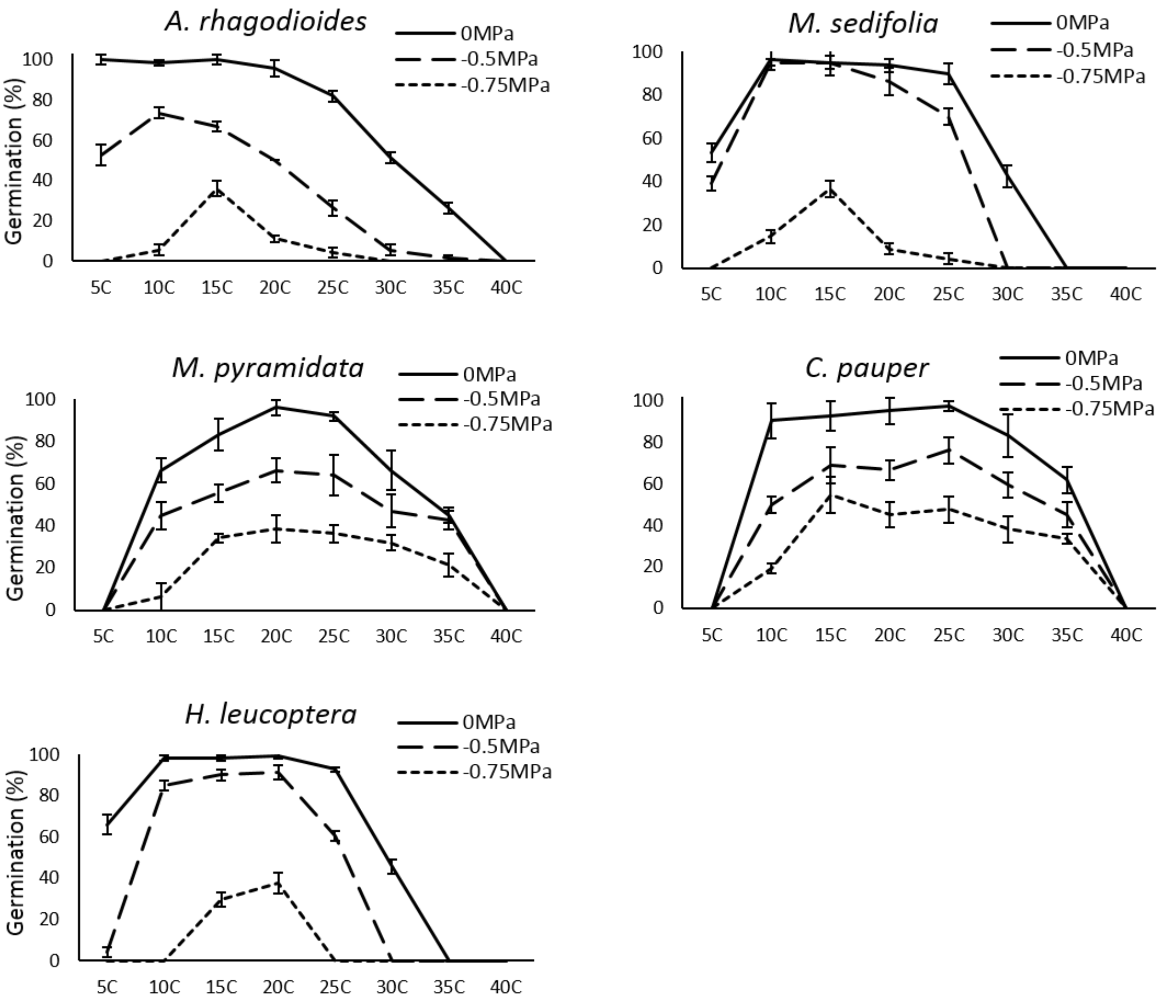

Fig 3.2: Final seed germination (mean ± standard error) of *A. rhagodioides*, *M. sedifolia*, *M. pyramidata*, *C. pauper* and *H. leucoptera* incubated under the combination of three water potentials (0, -0.5, and -0.75 MPa) and eight temperature treatments (5-40°C).

Three types of responses were observed regarding the viability of seeds exposed to temperature and water stress. Seeds were either killed by high temperatures of > 35°C (observed in *A. rhagodioides* and *M. sedifolia*), killed by negative water potentials of < -0.75 MPa (*C. pauper* and *M. pyramidata*) or, for *H. leucoptera*, remained viable after all temperature and water potential treatments (Fig 3.3). *H. leucoptera* exhibited great resilience to temperature and water stress, because nearly all seeds remained viable after the 30-day germination experiment at lowest water potential (-1.5 MPa), and at hottest (40°C) and coldest (5°C) temperatures tested.

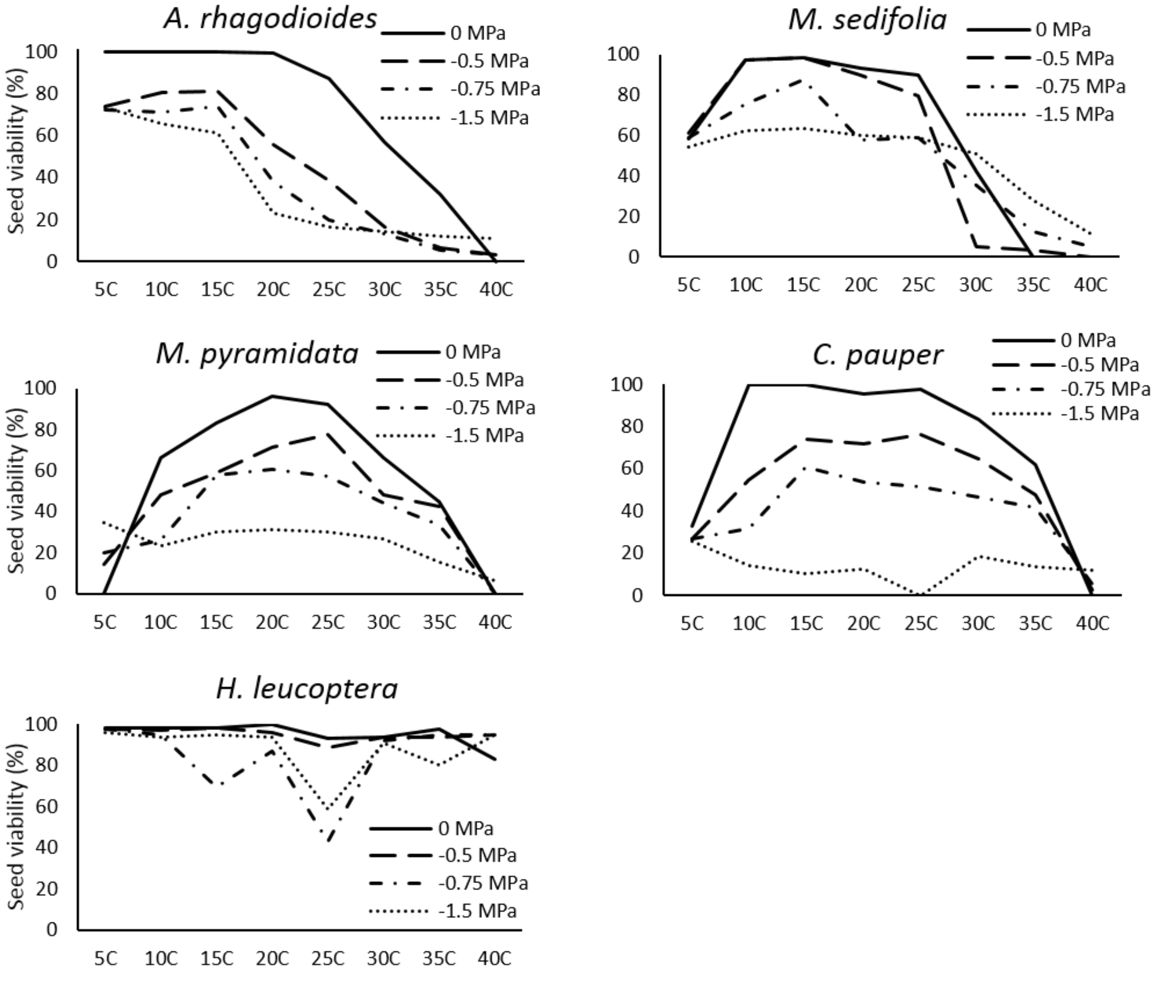

Fig 3.3: Seed viability of five species after 30 days of treatment at four different water potentials (0, -0.5, -0.75, and -1.5 MPa) and eight temperature treatments.

3.4.2 Germination speed is affected by temperature and water potential

For most species in this study, germination speed increased with increasing temperatures, and decreased with decreasing water potentials. The exception to this pattern was *H. leucoptera*, which showed germination speed increasing with temperature, until a peak in germination speed at 20°C that was followed by a rapid decline in germination speed as temperatures continue to rise (Fig 3.4). Time to 50% germination (t_{50}) values for *H. leucoptera* at -0.5 MPa were twice that at saturated conditions, exhibiting the greatest delays due to water limitation of the five species. The two *Maireana* shrubs were the fastest germinating species, with t_{50} values less affected by reduced water potential than observed in all other species. Water stress generally increased t_{50} values, and variation in t_{50}, and decreased maximum temperatures for germination. Delayed germination in response to reduced water potential were observed only at water potentials ≥ 0.35 MPa, and in conditions wetter than this, germination speed remained consistently high for all species.

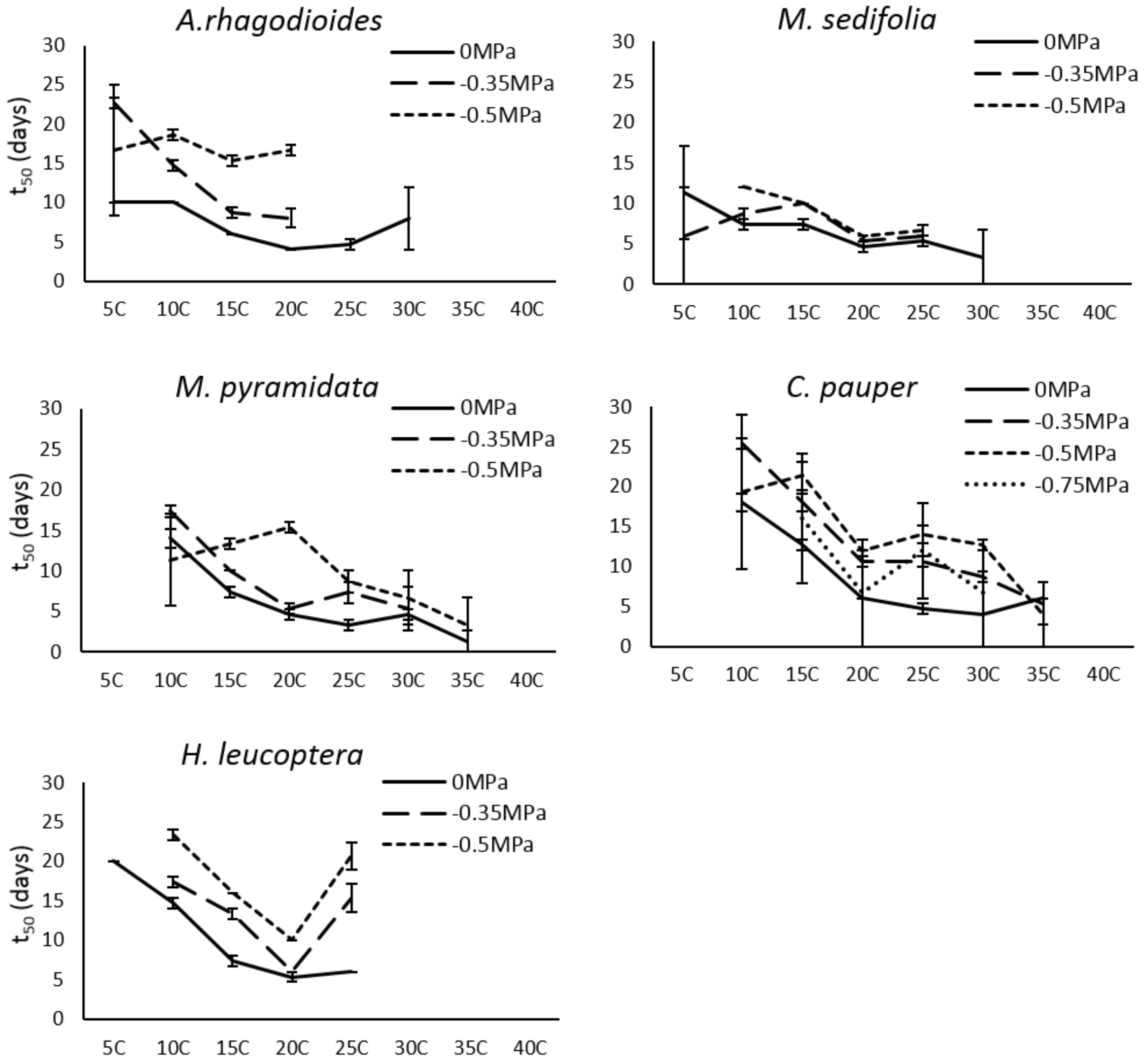

Fig 3.4: Time to 50% germination (mean ± standard error) of *A. rhagodioides*, *M. sedifolia*, *M. pyramidata*, *C. pauper* and *H. leucoptera* seeds incubated under different water potential (0, -0.5, and -0.75 MPa) and temperature treatments (5 - 40°C).

3.4.3 Cardinal temperatures and base water potentials for seed germination

For all species, base water potentials for germination revealed low germination when conditions are dry. The base water potential for 50% germination ranged between -0.61 MPa and -0.79 MPa, hence the driest condition at which seeds could germinate did not vary greatly between species. At temperatures above 20°C, *M. pyramidata* and *C. pauper* were able to germinate in the driest conditions, with the lowest base water potential for germination. All species had low germination proportions (≤ 10%) under low water potentials (-1.0 MPa) and no germination was observed at the lowest water potential tested, -1.5 MPa. There was no relationship between base water potentials for germination and seed mass ($R^2 = -0.32$, F = 0.035, p = 0.86, Fig 3.5). Average seed weight for *H. leucoptera* was 0.02g, and seed weights of all other species (Duncan et al. 2019) is available online at the TRY Plant Traits Database (see supporting information).

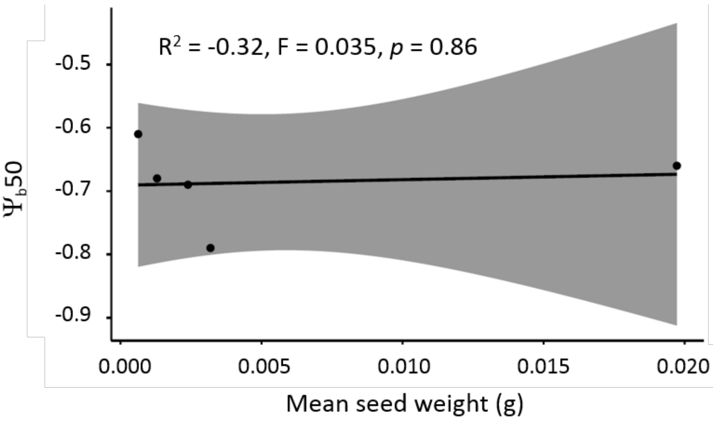

Fig 3.5: Linear model showing no relationship between mean seed weight (g) and base water potential to germination to 50% (Ψ_b50).

Cardinal temperatures for seed germination revealed all species, except *C. pauper* and *M. pyramidata*, had low base temperatures for germination ($T_b \leq 5$°C; Table 3.1, Fig 3.6). Optimum temperatures for germination ranged between 15°C and 31°C, and were highest for *M. pyramidata* and *C. pauper*. Maximum temperatures for germination were greatly reduced with water limitation in *A. rhagodioides*. Species were able to germinate in dryer conditions at 15°C or 20°C, whereas seeds required more moisture to germinate at temperatures above 25°C. All species showed higher germination proportions at optimal and sub-optimal temperatures, than at maximum temperatures for germination. At supra-optimal temperatures seeds were more sensitive to water stress, with germination proportions declining more rapidly in drier conditions at ceiling temperatures for germination.

Table 3.1: Minimum (*T_b*), optimum (*T_{opt}*) and maximum (*T_c*) temperatures for 50% germination at three water potentials. Results show cardinal temperature estimates (°C) from segmented models. The adjusted-R^2 of each segmented model is shown, as well as the standard error of T_{opt}.

Species	Segmented model adjusted-R^2	Cardinal temperatures(°C)		
		T_b	T_{opt}	T_c
A. rhagodioides				
0 MPa	0.93	-0.7	22.6 ± 1.1	34.7
-0.35 MPa	0.99	-0.8	20.0 ± 0.3	25.0
-0.5 MPa	0.99	-8.8	17.7 ± 0.4	25.0
M. sedifolia				
0 MPa	0.91	-4.1	25.0 ± 0.9	30.0
-0.35 MPa	0.77	1.5	24.6 ± 1.2	30.0
-0.5 MPa	0.89	2.7	24.1 ± 0.8	30.0
M. pyramidata				
0 MPa	0.64	6.5	15.0 ± 3.8	34.7
-0.35 MPa	0.92	5.7	22.4 ± 1.0	30.0
-0.5 MPa	0.66	3.4	24.8 ± 2.9	38.9
C. pauper				
0 MPa	0.97	7.2	31.4 ± 0.8	40.0
-0.35 MPa	0.94	2.9	32.8 ± 0.8	40.0
-0.5 MPa	0.90	3.4	27.0 ± 1.4	39.7
H. leucoptera				
0 MPa	0.92	2.7	22.7 ± 0.9	30.0
-0.35 MPa	0.84	5.3	20.0 ± 1.7	29.7
-0.5 MPa	0.96	4.8	20.1 ± 1-1	29.9

Overall, the hydrotime model was a good predictor of germination behaviour under water stress (Fig 3.7), with the majority of R^2 values exceeding 0.8 (Table 3.2). The hydrotime model often described germination behaviour at minimum and maximum temperatures better than it did at optimum temperatures. The model often failed to predict the consistently high germination of seeds at water potentials between 0 MPa and -0.5 MPa. Generally the hydrotime model predicted lower base water potentials for germination than observed by the data.

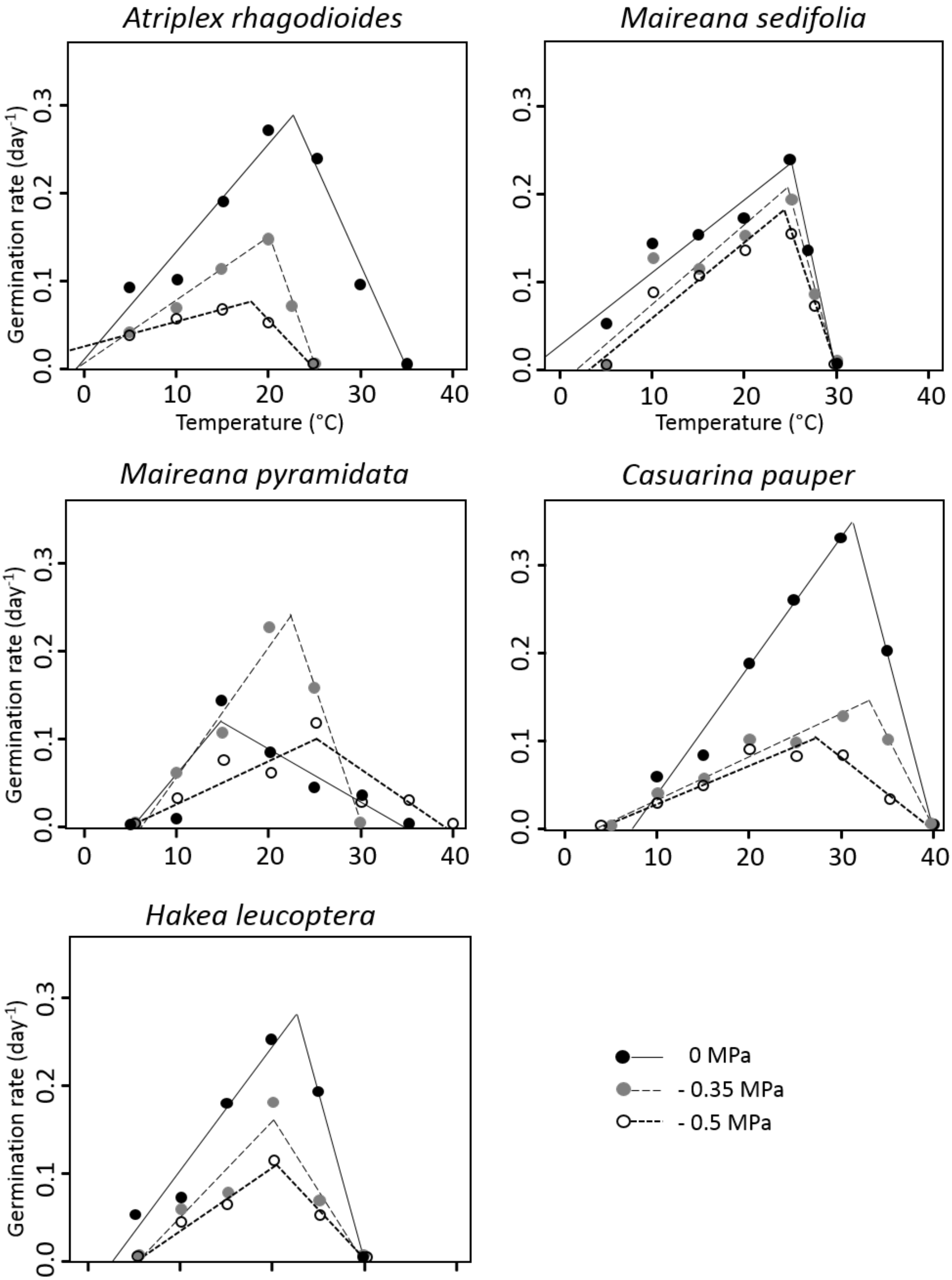

Fig 3.6: Rate of germination (to 50%) at three water potentials (0, - 0.35 and - 0.5MPa) and eight temperature treatments. Cardinal temperatures are estimated from the fitted segmented model; the lower and upper intercepts with the x-axis estimates T_b and T_c, respectively, whereas the break in the segmented model estimates T_{opt}.

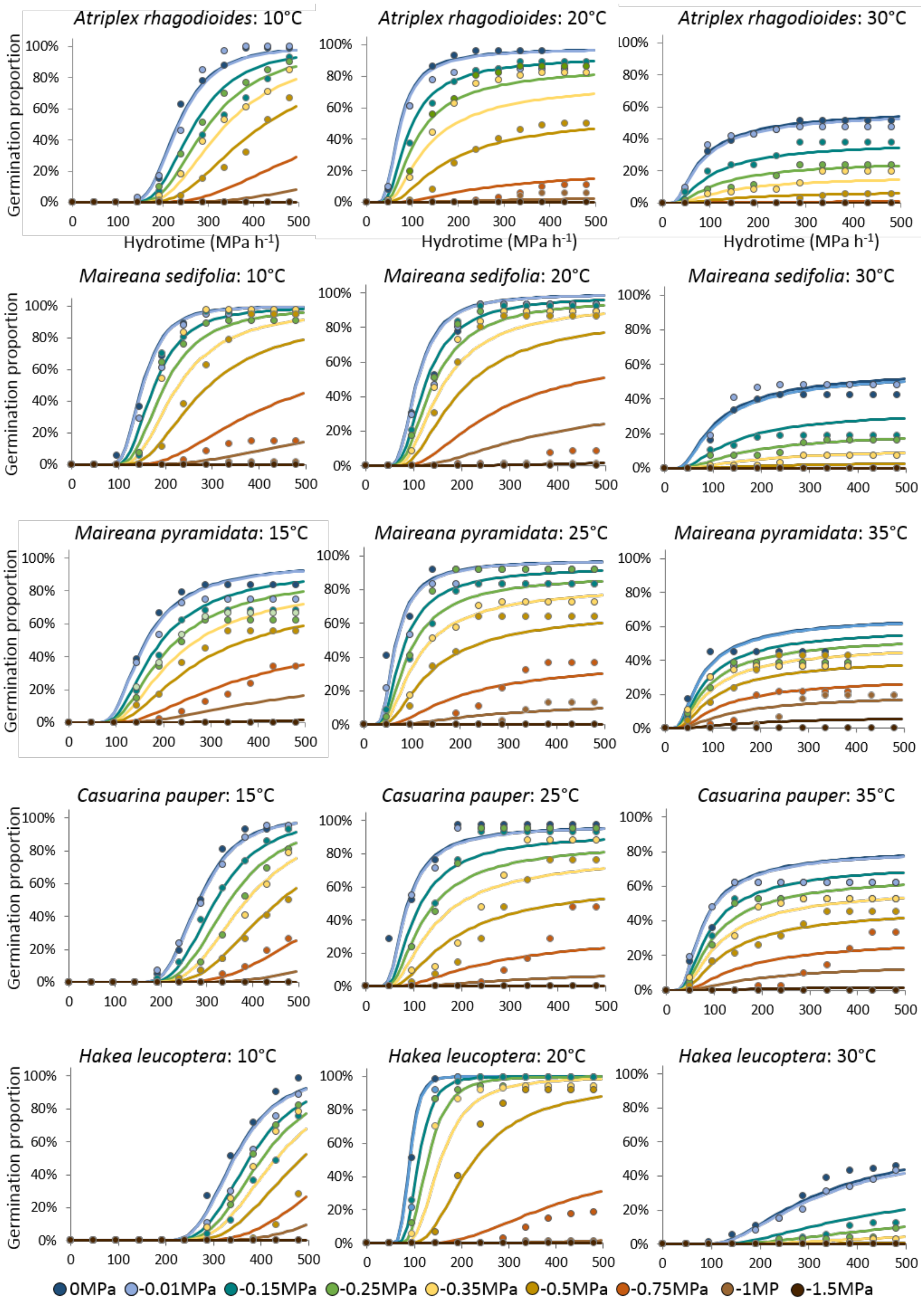

Fig. 3.7: Germination time courses across nine water potentials, with original germination data (dots) and hydrotime model predictions (lines) at three selected temperatures for each species (10°C, 20°C and 30°C for *A. rhagodioides*, *M. sedifolia* and *H. leucoptera*, and 15°C, 25°C and 35°C for *M. pyramidata* and *C. pauper*).

Table 3.2: Hydrotime required to 50% seed germination shows seeds accumulate more hydrotime under cooler conditions. θH = hydrotime (MPa h^{-1}) to germination to 50%, R^2 = determination coefficient, $\Psi_{b}50$ = base water potential to germination to 50% and σ = standard deviation of $\Psi_{b}50$ (MPa).

Species	**Hydrotime parameter**	**5°C**	**10°C**	**15°C**	**20°C**	**25°C**	**30°C**	**35°C**
A. rhagodioides	θH	170	260	95	49	41	21	52
	R^2	0.83	0.91	0.90	0.91	0.94	0.95	0.82
	$\Psi_{b}50$	-0.66	-1.11	-0.79	-0.61	-0.47	-0.07	0.19
	σ	0.24	0.29	0.22	0.27	0.33	0.30	0.50
M. sedifolia	θH	405	155	165	105	110	23	No germ.
	R^2	0.84	0.81	0.86	0.67	0.76	0.91	
	$\Psi_{b}50$	-0.81	-1.03	-1.19	-0.97	-1.32	-0.06	
	σ	1.14	0.27	0.34	0.35	0.61	0.25	
M. pyramidata	θH	No germ.	285	145	53	46	38	58
	R^2		0.89	0.92	0.72	0.85	0.86	0.80
	$\Psi_{b}50$		-0.98	-0.89	-0.70	-0.68	-0.47	-0.36
	σ		0.57	0.41	0.23	0.32	0.55	0.79
C. pauper	θH	No germ.	465	365	105	55	45	50
	R^2		0.91	0.93	0.86	0.62	0.88	0.87
	$\Psi_{b}50$		-1.14	-1.29	-0.83	-0.63	-0.62	-0.49
	σ		0.27	0.30	0.26	0.31	0.36	0.52
H. leucoptera	θH	285	580	110	74	77	77	No germ.
	R^2	0.90	0.83	0.64	0.85	0.86	0.87	
	$\Psi_{b}50$	-0.58	-1.69	-0.78	-0.83	-0.62	-0.12	
	σ	0.15	0.36	0.22	0.15	0.18	0.22	

3.5 DISCUSSION

This study demonstrates the importance of the interaction between temperature and water availability in the germination responses of arid plant species. To prevent seedlings emerging during dry conditions, we predicted high moisture thresholds for germination as the dominant trait among the species in our study. Indeed, for three species (*A. rhagodioides, M. sedifolia* and *H. leucoptera*) germination proportion and the thermal range for germination was drastically reduced when water potential was <-0.5 MPa (Fig 3.2). Germination of these species is likely limited to large and rare rainfall events. Conversely, some tree species from semi-arid regions of eastern Australia, *Eucalyptus cambadgeana* and *Acacia harpophylla* (Arnold et al. 2014a; Arnold et al. 2014b), and *Banksia* species from western Australia (Cochrane et al. 2014) are remarkably tolerant to water stress and germinate at water potentials as low as -1.5 MPa. However, these species occur in regions with seasonal rainfall regimes, where the chance of follow-up rainfall is higher and the risks associated to germinating from small rainfall events is reduced. *Casuarina cristata* was considered water-stress sensitive and showed no germination at water potentials below -0.75 MPa (Arnold et al. 2014b), similar to *C. pauper* and other species in this study. Many other arid species can germinate at remarkably lower water potentials than species in this study (Dürr et al. 2015; Hu et al. 2015; Shaygan et al. 2017), making them greater competitors when water is limited, and the hydrotime model predicted lower base water potentials for germination than actually observed. Hence, species in this study are generally considered water-stress sensitive, and avoidance of dry and hot conditions is a key trait enabling them to persist in an environment where rainfall events are usually small and unpredictable.

3.5.1 Germination speed reduced by water limitation

Rapid germination was observed in all species in this study at saturated conditions, and is an important advantage for arid species, because it enables them to capitalise upon the shorter pulses of water availability (Chesson et al. 2004). Germination rate for *A. rhagodioides* and *H. leucoptera* was greatly reduced by decreasing water potentials, taking twice as long to germinate at -0.5 MPa than at saturated conditions of 0 MPa. Slowed germination rate means seeds are exposed to a greater risk of seed death from desiccation, thus delayed germination has strong fitness consequences (Donohue 2005; Hoyle et al. 2015). However, significant delays in germination in response to water limitation may be beneficial if seeds can survive extreme conditions for extended periods of time, assuming they are not lost to predation (DeFalco et al. 2012). The risk-avoidance strategy is particularly beneficial to species with high seed longevity, including *H. leucoptera*, as seeds may remain in the canopy, or soil, until a large rainfall event occurs. Reduced germination proportion and speed under severely water-limited conditions observed in our study are consistent with previous studies (Joel and Oscar 2001; Van den Berg and Zeng 2006). This cautionary approach to germination due to water limitation is considered a special survival strategy used by arid species to reduce seedling mortality after low rainfall events (Zeng et al. 2010).

Rapid germination is an important strategy for arid seeds and small seeds generally germinate faster than heavy seeds (Gomaa and Picó 2011). However, larger seeded species are often found in dry environments (Baker 1972) and produce seedlings with greater survival and establishment rates in dry conditions (Leishman and Westoby 1994; Moles and Westoby 2004). This suggests that larger seeds are more drought tolerant, although few studies have explored the relationship between base temperatures and water potentials for germination and seed size. Certainly, some studies support this theory and show larger seeds have lower base water potentials for germination (Arène et al. 2017; Daws et al. 2008), which may enable them to exploit the advantages of increased survival rates at the seedling stage (Baraloto et al. 2005; Westoby et al. 1992). However, contrary to our prediction, there was no correlation between base water potential for germination and seed mass. Base water potentials for germination were similarly low for all species (Ψ_b50 = -0.61 MPa to -0.79 MPa), which suggests this is driven by the adaptive traits of arid seeds, rather than constraints in seed size, although our ability to ascertain the importance of the seed-size water-potential relationship is limited by the small number of species in this study.

3.5.2 Thermal ranges narrowed by water limitation

Temperature is an important factor for regulating the timing of seed germination, and thermal ranges for germination vary among biomes. Most species had wide temperature thresholds for germination, probably because the probability of rainfall is equal across all seasons. Certainly, T_b values were low for all species (<8°C), although T_c was lower for *M. sedifolia* and *H. leucoptera* than observed in most other native species (according to Dürr *et al*. 2015). This suggests that these two species have narrow thermal ranges for germination, which is driven by low T_c values. Water limitation altered temperature ranges for germination and generally induced two types of germination patterns; minimal changes to germination proportion and temperature thresholds for germination (*M. pyramidata* and *C. pauper*), or those with greatly narrowed temperature thresholds for germination and low germination proportions at low water availability (*A. rhagodioides*, *M. sedifolia* and *H. leucoptera*). Narrowed temperature ranges for germination due to water limitation further supports our first prediction that seeds are cued to germinate only in high moisture conditions.

We also expected seeds to show higher germination proportions in cool temperatures, and in all species they were. This demonstrates a higher tolerance of water stress when temperatures are cooler, allowing seeds to capitalise on lower evaporation rates at winter conditions. For example, there was a sudden drop in germination above 30°C for *A. rhagodioides*, *M. sedifolia* and *H. leucoptera*, which further supports selection for avoiding germination when evaporation rates are highest across summer. Negative temperature values for T_b reported here for *A. rhagodioides* and *M. sedifolia* are unlikely and exist because germination was high at 5°C for these species and the linear model has failed to capture the rapid drop in germination that presumably occurs between 0°C and 5°C. Regardless, germination at the coldest temperature tested (5°C) was high for *A. rhagodioides*, *M. sedifolia* and *H. leucoptera*, and supports our proposition that reduced germination at high temperatures is an important survival strategy for some arid species. We suggest that a preference for cooler temperatures and wet conditions are important characteristics of a risk-avoidance strategy because soil-moisture retention is greater in cold temperatures, thereby increasing the likelihood that seedlings emerge under optimal conditions for growth. However, soil temperature can be highly variable and influenced by soil surface humidity and moisture (Ashcroft and Gollan 2013), hence we recommend further studies testing the germination responses of seeds in field conditions.

Bet-hedging refers to a seed’s ability to remain dormant or viable in the soil across seasons without committing to germination, and allows seeds to forego synchronous recruitment until conditions are suitable for plant establishment (Gremer and Venable 2014; Simons 2009). It is commonly observed in seeds from arid zones (Fan et al. 2018b; Gremer et al. 2016; Lewandrowski et al. 2018) because, under low rainfall and high temperatures, germination is a high-risk event. These bet-hedging traits were observed in *H. leucoptera*; seeds have greater moisture requirements and lower germination proportions in hot conditions, and maintain high seed viability under physiological stress. *Hakea* is a serotinous species and has unusually high seed longevity (Duncan et al. 2019), hence risk of germination failure can be avoided despite being a non-dormant species. Having a reservoir of seeds in the soil or canopy that germinate upon wetting, but can survive if moisture disappears prior to germination, may enhance recruitment opportunities under unpredictable rainfall events. Further research is required to understand seed persistence and the prevalence of bet-hedging in a greater suite of arid zone species, and future studies should test these concepts in situ.

Serotiny enables species to control the timing of seed release with optimal conditions for seedling establishment, thus may be an important adaptation for arid zone plants. Serotiny levels in *H. leucoptera* are not yet reported and, considering the interdecadal fire regimes at the study site, seed release is likely triggered by seasonal temperatures and/or humidity, rather than fire (Bradshaw et al. 2011). *Hakea* have several other drought adaptations that reduce their dependence on seed germination success, such the ability to re-sprout from root suckers (El-ahmir et al. 2015), large seed size sizes (Groom and Lamont 1997) and sclerophyllous, needle shaped leaves (Barker et al. 1991) to prevent excess water-loss. Compared to other species in this study, *H. leucoptera* has a tendency for reduced seed germination in dry conditions which, we suggest, contributes to its reservoir of drought adapted traits (Lamont et al. 2016). Serotiny, seed longevity and high Ψ_b50 values are all traits that delay seed germination and reduce seed mortality during drought.

3.5.3 The risk-takers

The risk-taking germination strategy is simply to germinate readily and rapidly across a wide range of conditions, and in response to lower rainfall events. In this study, two species (*C.*

pauper and *M. pyramidata*) displayed these risk-taking characteristics. They maintained wide thermal ranges for germination at water limitation and had higher germination proportions (55% and 38%, respectively) in dry conditions (-0.75 MPa) than all other species. These species also had the highest maximum temperatures for germination at low water potentials and generally maintained rapid germination under water stress. Unlike *H. leucoptera*, both of these species had a large proportion of seeds die due to water limitation. This implies that *C. pauper* and *M. pyramidata* wager most of their seed reserves at each seeding event. However, for both species the risk-taking approach is advantageous because they seed reliably and frequently, and produce thousands of seeds at each seeding event (Callister 2004; Cunningham et al. 2011; Wotton 1993). The risk of population declines from extensive drought period is lessened by a steady supply of seeds, particularly for the long-lived tree species *C. pauper* that may have hundreds of seeding events throughout its lifetime. Theories suggest that higher functional plant species, such as perennial tree and shrub species, require larger rainfall events for establishment (Noy-Meir 1973; Schwinning and Sala 2004), yet these dynamics were not observed in this study as the slow-growing tree species, *C. pauper*, had similar moisture requirements for germination as *M. pyramidata*. Wide thermal and moisture envelopes for germination may explain the broader distribution in *C. pauper* and *M. pyramidata*. These two species also appear as the most dominant species of the region, hence a risk-taking strategy (assuming consistently high seed supplies are maintained) may be the more successful survival strategy in arid zones with unpredictable rainfall events.

The importance of water thresholds as a survival strategy appears to be linked to other reproductive adaptations and trade-offs of species in this study. For example, *C. pauper* and *M. pyramidata* produce seed more reliably and frequently than other species in this study, and high seed production could mediate the impact and risks associated with lower Ψ_b50 values for germination. Comparatively, flowering occurs very sparingly and irregularly for *M. sedifolia* (Wotton 1993), *H. leucoptera* (Barker et al. 1991) and *A. rhagodioides*, hence their lower base water potentials and lower base temperatures for germination would be beneficial traits to allow more conservative use of limited seed production. To further mediate the effect of infrequent seeding events, *A. rhagodioides* has physiologically dormant seeds and *Hakea* have serotinous seeds that are generally long-lived, and have higher Ψ_b50 values under increasing temperatures. Based on these results, we suggest that species that frequently and reliably produce seed can afford riskier germination strategies, such as germinating at lower water potentials, as the consequences of failure to establish are less dire than for species that do not reliably produce seed. Conversely, species with unreliable seed production avoid risk by limiting germination to wet conditions. We recommend further studies for a greater suite of arid species to test this relationship.

3.5.6 Implications for restoration

As this study demonstrates, seed germination in arid zones is limited by high temperatures and low moisture availability, and these factors have been linked to poor recruitment outcomes from restoration efforts (Chesson et al. 2004; García-Fayos et al. 2000). However, water limitation impacts species in different ways and, for those that have high Ψ_b50 values and avoid germination during dry conditions, restoration from seeding efforts alone remains challenging when rainfall is unpredictable. Reestablishment of species that avoid germinating in hot and dry conditions, such as *A. rhagodioides*, *M. sedifolia* and particularly for *H. leucoptera*, should be managed as water-stress sensitive species with episodic recruitment. These species likely germinate following large rainfall events, which are rare in arid zones. Population models predict that only between 1.6 – 3.7 large recruitment events per century are necessary to sustain plants populations with episodic recruitment, and according to the semi-stochastic model, an annual probability of 50% that small recruitment events are needed (Wiegand et al. 2004). For such species, further studies are required to investigate alternative intervention measures to support restoration (e.g. irrigation), and to understand the influence of climate change on the recruitment of water-stress sensitive species in arid zones. Large-scale restoration methods usually involve a once-off application of seed (Corbett 1999), typically during autumn, when soil temperatures are still relatively warm and evaporation rates are lower. Our results suggest that cooler temperatures may enhance recruitment opportunities for drought avoiding species in arid regions. Germination times may be marginally lengthened by cool temperatures but evaporation rates are lower, thus ensuring higher water retention in the soil profile beneficial for germination. Perennial species in this study exhibit varying responses to low moisture availability, suggesting that a ‘one for all’ approach may not be suitable for the restoration of all arid zone species. Our results have demonstrated the physiological thresholds for germination of our study species, as determined in laboratory conditions. Further research should look to test these ideas in the field, where temperature, moisture and other environmental filters can rapidly fluctuate, impacting the germination responses of seeds.

CHAPTER 4

Soil reconstruction after mining fails to reinstate properties crucial for vegetation recovery in arid Australia

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Running title: Soil reconstruction for arid vegetation recovery

Acknowledgements: We wish to acknowledge the environmental team at Tronox Mining for funding this project, installing soil pits, and providing instrumental support and access to land. We thank Wolfgang Lewandrowski from Kings Park Science, and The University of Western Australia, for providing a critical review of this manuscript.

4.1 ABSTRACT

Background and Aims: The biogeochemical properties of soils drive ecosystem function and vegetation dynamics, but few studies have measured their role in arid ecosystems. The aim of this study is to assess soil structure in two vegetation-types in an arid ecosystem, and to understand how these soil properties compare to a reconstructed soil profile after mining.

Methods: In an arid ecosystem in southeast Australia, soil samples were collected at five depths (to 105 cm) from remnant woodland and shrubland sites, and sites either disturbed or totally reconstructed after mining. We assessed soil physico-chemical properties, and tested if microbial activity increases with time since restoration.

Results: Soils in the remnant arid ecosystem had course textured topsoils that overlay clay horizons, which is important for reducing water loss from evaporation and deep drainage. Conversely, reconstructed soils had high sand content at subsoil horizons and unfavourably high bulk density and compaction at surface layers (0 – 20 cm). Reconstructed soils had topsoils with higher pH and electrical conductivity. Microbial activity declined with time since restoration, indicating that soil reconstruction disrupts microbial populations in surface biocrusts.

Conclusions: Soil reconstruction disorganises soil horizons and properties that control rainfall infiltration and water storage in arid zones, particularly the distribution of clay content and ions. Future restoration efforts should focus on increasing sand content of soils near the surface, to reduce evaporative water loss and improve soil quality and plant health.

Keywords: Arid zone restoration, biochemical properties, inverse texture, microbial biocrusts, soil profile, topsoils.

4.2 INTRODUCTION

Land degradation and desertification are major global socioeconomic and environmental issues (Wang 2004; Zhang et al. 2005). Restoration of degraded arid zones is particularly challenging due to low and variable rainfall (Pickup and Stafford Smith 1993). Despite enormous efforts, restoration success in arid ecosystems is low (e.g. Cortina et al. 2011; Madsen et al. 2016; Ravi et al. 2010). Restoration is often complicated by nutrient-poor skeletal soils, erosion from wind and water, and a sparse distribution and cover of slow-growing plant species (Kassas 1995). Additionally, limited water availability restricts plant productivity (Noy-Meir 1973), which makes these ecosystems more sensitive to disturbance, and more challenging to restore than ecosystems with higher rainfall (Constantini et al. 2016; James et al. 2013). Yet the restoration of arid ecosystems remain understudied, and a lack of understanding of landscape processes contributes to poor restoration outcomes (Yirdaw et al. 2017).

Water is the major limiting resource for growth and productivity in arid zones (Noy-Meir 1973) because rainfall is low and evaporation is often higher than rainfall across all months (Houston 2006). Arid soils have characteristics that influence water loss and enhance the temporal availability of water following rainfall (Reynolds et al. 2004; Sala et al. 1988). Specifically, physical soil properties such as compaction, bulk density, clay content and horizon thickness, directly influence infiltration and evaporation (Simmers 2003). According to the inverse texture hypothesis, arid vegetation is more productive in coarse-textured soils than fine-textured soils due to reduced evaporative water loss in the former (Noy-Meir 1973; Sala et al. 1988). Conversely, high bulk density and fine particle content at lower soil horizons prevents water leeching to regions below the maximum rooting depth of plants. Soil texture drives soil-water storage (Jia et al. 2013), which in turn strongly affects plant productivity and community dynamics in arid ecosystems (Cleverly et al. 2016). Consequentially, any disturbing process that removes and reorganises soil structure can impact the ability of the soil to resist water loss, and can negatively impact plant growth.

Mining has the potential to completely transform soil chemical and physical profiles in post-mined landscapes (Sheoran et al. 2010). Mined soils typically have lower nutrient availability (Akala and Lal 2001), higher bulk density and lower porosity (Chong et al. 1986), and higher pH and electrical conductivity (Shrestha and Lal 2011). These soil properties are crucial components influencing the soil-water balance and distribution of plant species in arid zones (Allen et al. 1997; Huang et al. 2017). Excavating and relocating soils also reduces the amount of topsoil and subsoil returned to the landscape (Sheoran et al. 2010), because the surface area to be restored is often larger than the area disturbed. Suboptimal storage conditions of the topsoils can also cause significant erosion and loss of soil (Golos and Dixon 2014). Additionally, as reconstructed soils are often dissimilar to pre-existing profiles, significantly altered soil physico-chemical properties can further influence resource dynamics (Muñoz-Rojas et al. 2016). Soils in this condition negatively influence plant and ecosystem productivity (Grigg et al. 2010; Liu et al. 2013; Lowery and Schuler 1994), and the ability of native species to adapt to local conditions (Griscom and Ashton 2011). Despite the importance of soil properties to the establishment and survival of arid plants (Austin et al. 2004; Gebauer and Ehleringer 2000), we still lack empirical studies that compare soil properties in remnant and severely disturbed arid ecosystems.

Clearing vegetation and stripping topsoils degrades the soil microbiome and, although often overlooked within the context of restoration, microbial activity in arid zones is a critical factor for plant fitness and diversity (Lau and Lennon 2012; Moreira-Grez et al. 2019; Wagg et al. 2014). Microbial activity in biocrusts is important for soil stability, nutrient cycling and moisture retention (Gypser et al. 2016; Lau and Lennon 2012; Makhalanyane et al. 2015). Recovery of microbial crusts on bare soil is incredibly slow (Kade and Warren 2002), and may require hundreds of years to fully recover (Belnap and Eldridge 2001). Vegetation cover can exert significant influences on microbial activity, subsequently altering the biogeochemistry of soils and ecosystem function (Johnson et al. 2016). Hence, there are positive (Butterfield and Briggs 2009; Johnson et al. 2016) and negative (Sharma and Tongway 1973) feedbacks between vegetation cover, microbial activity and soil fertility (Bezemer et al. 2006; Mehrabi et al. 2015). However, despite their significance to restoration, feedbacks effects between vegetation dynamics, microbial activity and soil properties are still poorly understood (van der Putten et al. 2013).

The aim of the study is twofold: (1) to assess soil structure and properties in a natural arid ecosystem, and (2) to understand how soil properties important for plant growth are impacted by severe disturbance and soil reconstruction. Based on the prediction that changes to soil physical, chemical and biological structure impede plant recovery and inhibits growth of trees and shrubs (Schwinning and Sala 2004; Sheoran et al. 2010), we test three hypotheses: (1) that reconstructed soils differ from the undisturbed, remnant soils in properties important for plant growth, specifically in the distribution of particle-size content and nutrients, (2) that the reconstructed soils are more similar to shrubland than woodland sites due to plant-soil feedback mechanisms, and (3) that microbial activity in the reconstructed soils increases with time since disturbance.

4.3 MATERIALS AND METHODS

4.3.1 Study area

The study site was located 30 km west of Pooncarie in south-eastern Australia's arid zone (33°22'S, 142°13'E). Mineral sand mining occurs in the region, and this study was conducted at the Ginkgo Mine. Mining operations commenced at the Ginkgo Mine in 2006 and are due to conclude in 2020, although rehabilitation efforts will continue beyond 2020. Relief across the site varied by approximately 10 m with average elevation of approximately 70 m above sea level. The study area is a hot desert climate, according to the Koppen Classification System. Across 60 years of climate data, average annual rainfall was 250 mm (BOM 2018), although annual rainfall often falls below 200 mm for consecutive years (Environdata 2019). Mean annual temperature is 18°C, and temperatures during the study period ranged from 2–47°C. Evaporation rates (mean 5.6 $\mathrm{mm.hr^{-1}}$) are higher than rainfall across all months (Environdata 2019). Soils of the study area are Pleistocene age aeolian deposits of the Woorinen Formation and arranged mostly as plains (Lawrence 1966), but also occur as east-west aligned dunes and swales. Soils are predominantly Calcarosols (Isbell and National Committee on Soil Terrain 2016) with surface soil textures of plains dominated by sandy clay loam and clay loam, with subordinate dune areas often characterized by light sandy clay loam and sandy loam. Subsoil B-horizons are ubiquitously characterized by carbonate pedoderms with elevated calcium carbonate content. Soils of rehabilitation areas are Anthroposols (Isbell and National Committee on Soil Terrain 2016). Native keystone shrubs have been successfully established in rehabilitation areas, but successful establishment of tree species has been negligible (Sluiter and Schultz 2017).

4.3.2 Site selection

In this study, we selected sites to monitor in three types of soil profiles that remain after mineral sand mining, each of which is subject to ecological restoration: (1) mine path sites, where soils have been totally removed, stored and replaced with reconstructed subsoil and topsoil; (2) overburden sites, which are raised structures where subsoil and topsoils were reconstructed over excess rock fragments; and (3) soil stockpile sites where subsoils and topsoils that were excavated from the mine path were temporarily stored, and then removed for restoration across mine path and overburden areas (Fig 4.1). The mine path and overburden sites were considered as reconstructed soil profiles herein. In the soil stockpile sites, only the surface layer had been disturbed and hence these sites will be considered separately. Mine path and overburden sites were reconstructed by spreading a minimum of 20 cm subsoil and 20 cm of topsoil prior to seeding (Fig 4.1). Restoration activities (including direct-seedling with a mix of native plant species) occurred in distinct phases over four years in overburden sites (2009, 2011, 2012 and 2013), and over three years in mine path and soil stockpile sites (2014, 2015, and 2017). To understand how soil reconstruction impacts properties important for plant development, three sites were selected within each of the three categories of disturbance within the mined area. The exception was the overburden site, where an additional site was included (n = 4). Five remnant shrubland sites and five remnant woodland sites were also selected from around the study area for comparison to the mine sites.

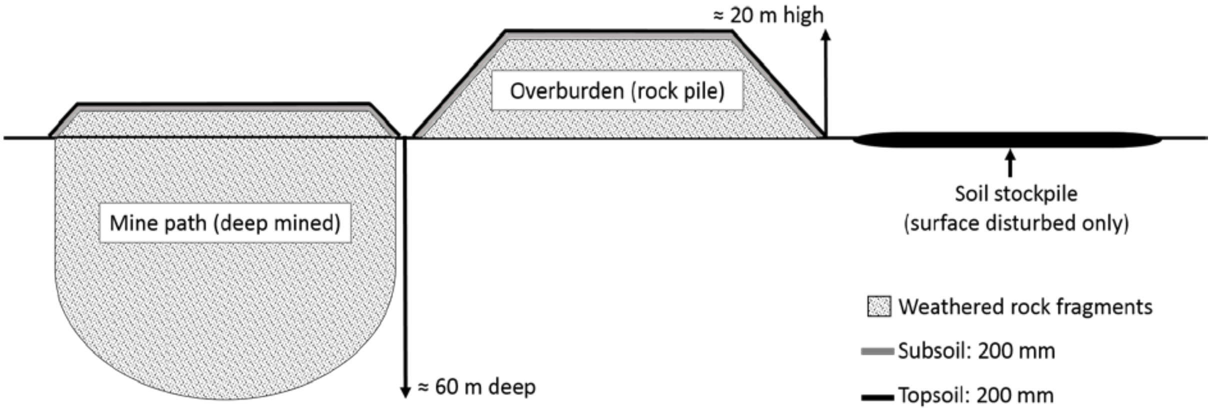


Fig 4.1: Soil profile types at the study site. Mine path sites were excavated to below groundwater depth, and the mine pit is then filled with rock fragments and topped with subsoil and topsoil. Overburden sites are mountains of excess rock fragments, also topped with subsoil and topsoil. Soil stockpiles are where top soils are removed at the beginning of mining and temporarily stored until they are returned to mine path and overburden sites; this process disturbs the original topsoil layer of these sites.

4.3.3 Vegetation of the study area

The two dominant broad vegetation community types are (a) woodlands dominated by belah (*Casuarina pauper*) with a bluebush (*Maireana* spp.) understorey shrub layer; and (b) chenopod shrublands primarily dominated by *Maireana* species. Shrubs were observed across all sites, although shrubs were typically smaller at woodland sites. The shrub layer of the vegetation is dominated by one of either *Maireana pyramidata* or *M. sedifolia*, and seldom both. These two species are long-lived perennials which grow to 1.5 m (Walsh 1996) and in the case of *M. sedifolia*, may live for centuries (Crisp 1978). Other common perennial chenopod shrubs present include *Maireana georgei*, *M. turbinata* and *M. trichoptera* and *Atriplex* spp., including *A. vesicaria* and *A. stipitata.* Only the woodlands featured tree and grass species, and these sites were dominated by the tree *Casuarina pauper* and the perennial grass, *Austrostipa nitida*. Both of these species were absent from rehabilitation sites. The most common ground flora species across all sites was the short-lived perennial herb, *Sclerolaena obliquicuspis.* The most prolific weed across all sites was *Carrichtera annua*, or Ward's weed, which was more prevalent in the reconstructed ecosystems. Current vegetation structure at the reconstructed sites was more similar to shrubland than woodland sites, despite the broadcasting of significant quantities of tree and grass species, to seed reconstructed soils, that fail to establish.

4.3.4 Soil description

Soil profiles of remnants and rehabilitation sites were described using the Australian Soil Classification (Isbell and National Committee on Soil Terrain 2016), by excavating a pit with a backhoe to 1.5m depth. At every pit site, all soil horizons were identified using the following criteria: soil texture, colour, pedality (type and grade), field pH, readily available water at maximum root zone depths (herein referred to as available water) and carbonate reaction type. Soil samples were collected by scraping soil from the pit face with a small pick hammer at depths of 0–10 cm, 10–20 cm, 25–45 cm, 55–75 cm and 85–105 cm. Soil samples were stored at 4°C immediately upon collection, and during transportation to the laboratory, until processed and analysed.

4.3.5 Chemical properties of soils

Soil physical and chemical properties were measured by APAL Agricultural Laboratory (Adelaide, Australia) which analysed the following soil chemical properties according to Rayment and Lyons (2011): soil pH was measured via the 1:5 soil-water suspension method, determined after shaking for one hour at 25°C, and the 1:5 soil/0.01 M calcium chloride extract method with stirring during measurement. Electrical conductivity (EC) was determined using the 1:5 soil/water extract method, using air-dried (40°C) soils shaken for 1 hour at 25°C. Effective cation exchange capacity (eCEC) is the sum of exchangeable bases plus exchange acidity and was calculated as follows: ECEC (c.mol/kg) = exchangeable bases (Ca^{2+}+ Mg^{2+} + Na^+ + K^+) + exchange acidity (Al^{3+} + H^+). Chemical components of exchangeable bases were measured using the 1 M ammonium acetate method and exchange acidity components by the 1 M potassium chloride method. Results were determined by atomic absorption spectrometry and reported as exchangeable cations (c.mol/kg) on an oven-dry basis. Bicarbonate-extractable phosphorus (Colwell-P) was determined with automated colour and continuous segmented flow (Rayment and Lyons 2011). Bicarbonate-extractable K^+ tests were also applied to measure Colwell potassium. Results were determined through atomic absorption spectrometry and reported as extractable K and P (mg/kg) on an air-dry basis. Total nitrogen was calculated using the dumas high-temperature combustion method, using high-grade EDTA ($C_{10}H_{16}N_20_8$) dried at 105°C for 2 hours. Mineral nitrogen, including nitrate and ammonium, was measured with 2 M KCl, automated colour, and continuous segmented flow, and reported as NH_4^+ and NO_3^- (mg N/kg). Total organic carbon (TOC) was determined through dumas high-temperature combustion, which analyses the amount of CO_2 liberated from combustion at 1050-1200°C. Calcium carbonate equivalent was calculated through rapid titration, where soils treated with 1 M hydrochloric acid were titrated with 0.5 M sodium hydroxide.

4.3.6 Biophysical properties of soils

Soil bulk density is the ratio of the mass of oven-dried soils to the bulk volume of the soil ($D_b = M_s/V_t$) and samples were collected using a 10 cm corer knocked into the pit face at 5 cm, 15 cm, 35 cm, 65 cm and 95 cm. To measure bulk density, gravimetric soil-moisture and soil porosity according to Carter and Gregorich (2007), soil samples were oven dried at 105°C until soil mass remained constant. The structural stability of soil aggregates was measured using the Emerson (1967) test. Slaking was noted after 1 minute and then after 1 hour and dispersion was noted after 1 hour and then again after 20 hours. All samples that showed no dispersion as aggregates were re-worked and a sample placed in de-ionised water. The plates were then examined after 1 hour. Soil compaction along each pit face was measured using a pocket penetrometer, with three measurements taken at 5 cm, 15 cm, 35 cm, 65 cm and 95 cm. Surface soil compaction was also measured with a pocket penetrometer, and six soil surface penetrations were performed at every 50 cm along a 3-m transect.

4.3.7 Microbial activity of soils

Samples collected for analysis of microbial activity were stored at 4°C upon collection, then frozen within 4 hours of collection, transported, and stored frozen until the analysis was complete. Soil samples for analysis of microbial activity were collected from one depth only, 0–15 cm, using a 26-mm soil auger. The auger was moved out in a spiral pattern, until 25 samples were collected at each site. Samples were extracted into a bucket, which was thoroughly blended by pouring into another bucket and transferring 10 times. To estimate microbial activity in soils, the microbe activity wise (MAWS) test was used to measure the CO_2 emitted from microbes, also their respiration rate, over an incubation period. The MAWS test was conducted by Microbiology Laboratories Australia Pty Ltd.

4.3.8 Statistical analysis

Differences in soil properties were tested at two levels: (1) among site types (mine path, overburden, soil stockpile, shrublands and woodlands) and (2) at a broader ecosystem level, to test for differences between reconstructed soils (mine path and overburden sites grouped) and remnant soils (shrublands and woodlands grouped). Soil stockpile sites were excluded from the ecosystem level analysis, as they did not fit either the remnant or reconstructed categories. A Kruskal-Wallis test (which considers pairwise comparisons of means for non-parametric samples) was used to test differences among site types, and the Mann-Whitney test was used for the ecosystem-level test. To investigate the correlation between soil properties and sites, we performed a correlation-based Principal Components Analysis (PCA), based on normalised data and Euclidean distance. We tested for differences between woodland and shrubland sites in mean topsoil depth, observed root zone depths, and available water using t-tests. Correlations between available water, topsoil depth and observed root zone depth, and correlations between microbial activity and time since restoration, were assessed using Pearson tests. All statistical analyses were performed using SPSS (IBM Corp 2017), except for PCA which was performed using CANOCO 5.0 (ter Braak and Šmilauer 2012).

4.4 RESULTS

4.4.1 Physical properties of topsoils

Fine particle content at all remnant sites showed coarse topsoil overlying finer-textured subsoil, demonstrating a highly organised soil profile (Fig 4.2); topsoils at these remnant sites ranged from sandy loam to sandy clay loam (10–30% clay content) and, at depths below 85 cm, subsoils were classified as light clay or light medium clays with 35–40% clay content. In contrast, the reconstructed soils did not demonstrate this organisation of the soil horizons; four sites had the largest soil particles in the profile at subsoils below 85 cm, and three overburden sites had a course soil texture throughout the entire profile (Fig 4.2). The only reconstructed site to exhibit similar patterns to remnant sites in the distribution of particle-size content (course topsoil with fine-textured subsoils) was the oldest overburden site, which was reconstructed in 2009.

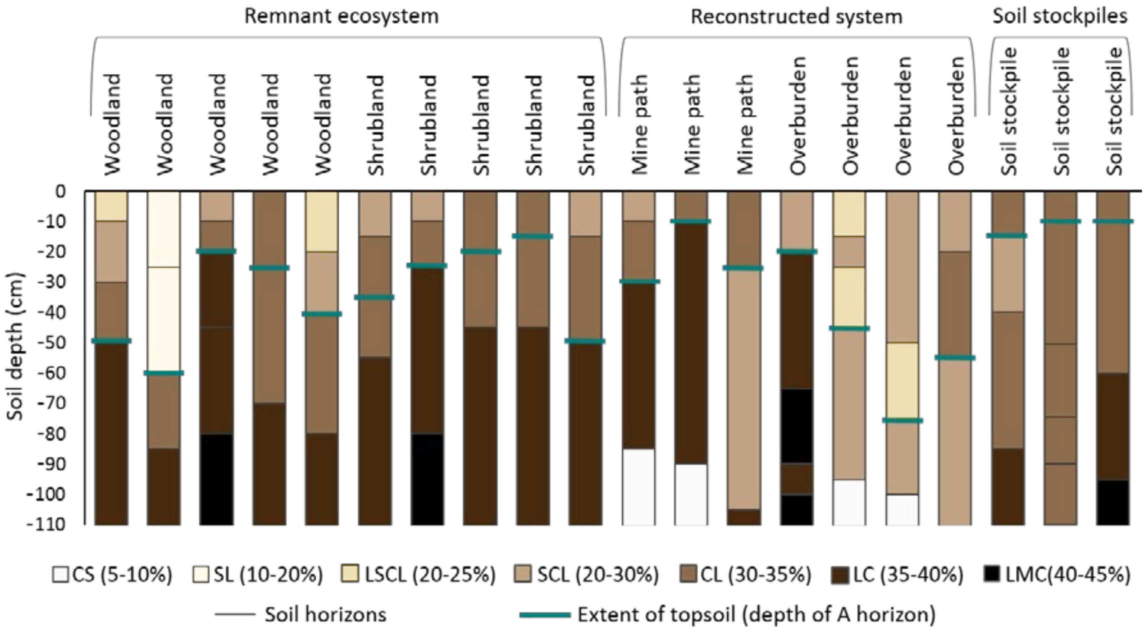


Fig 4.2: Soil horizons and clay content observed at all sites. Woodland and shrubland sites are from the remnant ecosystem, and mine path and overburden sites have soils that are reconstructed after mining. Soil stockpile sites had only the surface layers of soils disturbed. CS = clayey sand, SL = sandy loam, LSCL = light sandy clay loam, SCL = sandy clay loam, CL = clay loam, LC = light clay and LMC = light medium clay. Clay content of each texture class is shown in parentheses. The colour scale used for soil layers (from light to dark) represents increasing clay content, from light to dark.

Overall, soils were classified as clay loam, with a subangular blocky pedality. All soils were prone to slaking, but experienced little to no dispersion. Subsoil horizons were classified as Bk (indicating the accumulation of calcium carbonates). Reconstructed sites contained a relatively shallow C horizon, with weakly consolidated sediments and a lack of aggregation. Topsoil depth was highly variable among sites and treatments. Topsoil depth ranged from 20–60 cm in woodlands, and from 15–50 cm in shrubland sites (Fig 4.3). Reconstructed sites had highly variable topsoil depths. Soil stockpile sites had the lowest topsoil depth, with only 10–15 cm of topsoil, which was significantly lower than observed in overburden sites (p = 0.041). Across all sites, there was a positive correlation with topsoil depth and available water at maximum root zone depths (p = 0.018, Fig 4.4a), with topsoil depth explaining 52% of the variation in available water. Similarly, root zone depth and available water at maximum root zone depth were positively correlated (p = 0.002; Fig 4.4b), although there was no correlation between root zone depth and topsoil depth (p = 0.641).

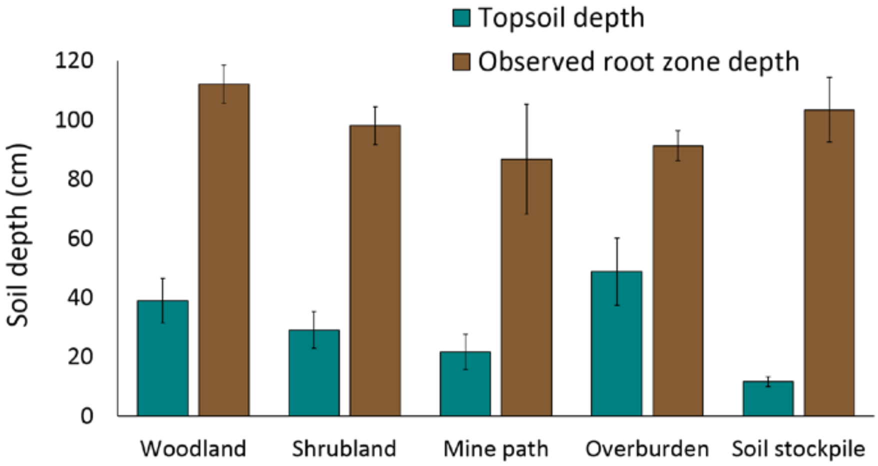


Fig 4.3: Topsoil depth and observed root zone depth (± SE).

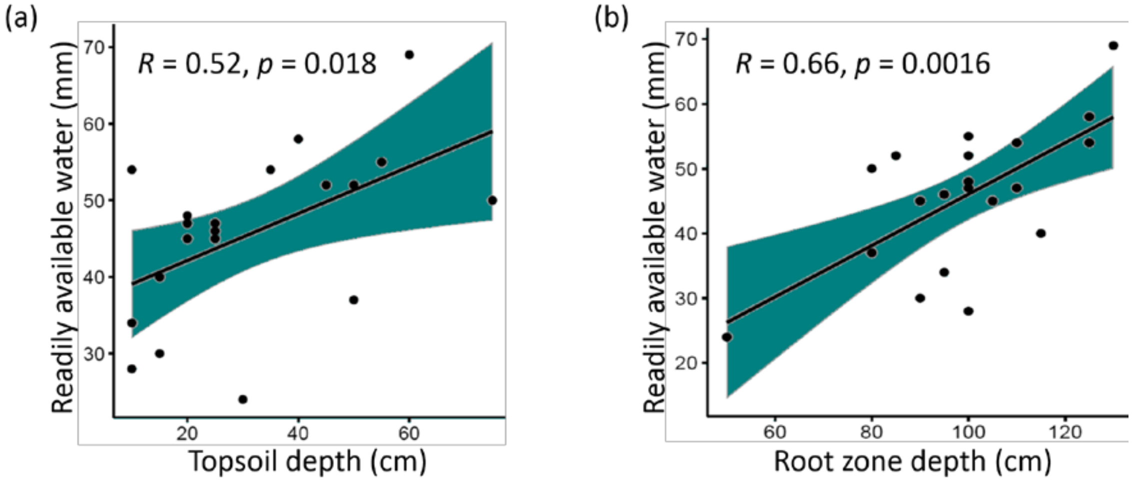


Fig 4.4: Correlations between readily available water at the maximum root zone depth and (a) topsoil depth and (b) root zone depth.

4.4.2 Compaction and bulk density

Surface compaction was higher in remnant soils than in reconstructed soils (Fig 4.5a). Compaction throughout the soil profile, at depths below 5 cm, generally increased progressively with soil depth at all sites. Mean bulk density along the soil profile at remnant sites was generally consistent, though not at reconstructed sites or soil stockpiles (Fig 4.5b) Bulk density was very high at 15 cm in reconstructed soils and, at this depth, bulk density at one mine path and two overburden sites was > 2.0 g/cm^3 (at one overburden site, bulk density at 15 cm was 2.3 g/cm^3). Bulk density was higher in mine path soils at depths below 35 cm than at all other sites.

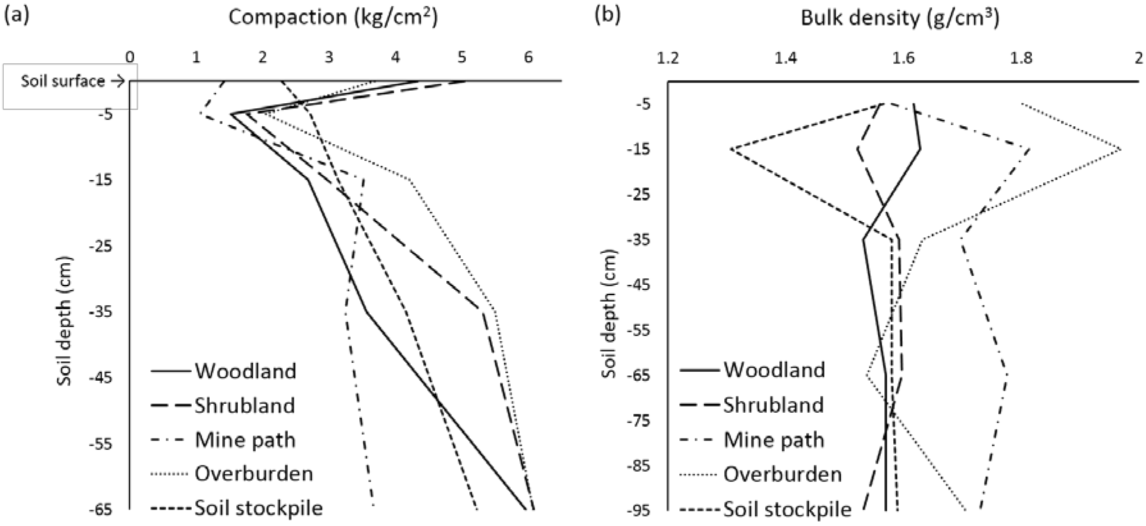


Fig 4.5: Mean compaction and bulk density at all sites. (a) Compaction was recorded at the soil surface, and throughout the soil profile, although depths below 65 cm are not presented because compaction exceeds maximum reading of the penetrometer at most sites, at soil depths >65 cm. (b) Bulk density was recorded throughout the soil profile, although not at the soil surface. Error bars are removed from charts to improve visibility, and standard error for mean bulk density are presented in table 4.1.

4.4.3 Soil chemical properties

Soils were low in nutrients at all sites, although differences were observed among sites in the distribution of chemical properties through the soil profile. All sites were very low in total organic carbon and nitrogen, and in ammonium nitrogen which was generally less <2 mg/kg. Total nitrogen, potassium and Ca:Mg generally decreased with soil depth, the latter due to an increase in magnesium with soil depth. Soils were non-saline, indicated by elctrical conductivity values below 1.5 dS/m. Soil pH increased with depth and ranged from 7.6–8.4 across all sites, with topsoils and subsoils considered moderately to strongly alkaline (Wetherby 1994). Remnant and reconstructed soils varied significantly in terms of their soil chemical composition (Table 4.1). At 10–20 cm, bulk density, total organic carbon, pH, electrical conductivity, total nitrogen and calcium carbonate were significantly different among treatments. Electrical conductivity and cation exhange capacity were generally significantly higher in mine path than woodland sites at depths between 0– 45 cm. Electrical conductivity (salinity; dS/m) was significantly higher in reconstructed soils at all depths from 0–75 cm and pH was significantly higher in mine path and overburden sites at 0–20 cm (Table 4.1). Differences between remnant and reconstructed ecosystems in topsoil depth, observed root zone depth and available water were not significant (P = 0.74, P = 0.09 and P = 0.28, respectively).

The reconstructed soils were most easily differentiated from the remnant soils based on variables associated with salts; soil properties that were the most influential in explaining variation between treatments, as shown in the PCA diagrams (Fig 4.6), include cation exchange capacity (eCEC), electrical conductivity (EC), calcium, magnesium, potassium, calcium carbonate, and pH. Remnant woodland and shrubland soils had similar soil properties, and were different from reconstructed soils, particularly at surface (0 cm – 20 cm) and lowest (55 cm – 105 cm) soil depths; remnant soils in the PCA diagrams were clustered at these depths showing greater homogeneity in soil properties compared to the reconstructed soils, which were more-widely dispersed across the axes at each depth

Table 4.1: Soil chemical properties at different soil depths (± standard errors). BD = bulk density (g/cm^3), Moisture = (%), TOC = total organic carbon (%), pH = pH level following CaCl2, EC = electrical conductivity (dS/m), eCEC = effective cation exchange capacity (c.mol/kg), Na = Sodium (mg/kg), Nitrate N = nitrate nitrogen (mg/kg), Total N (%), K = Colwell potassium (mg/kg), Ca:Mg = calcium to magnesium ratio (%) and $CaCO_3$ = calcium carbonate (%). Significance levels of differences in soil properties at the site level, and at the ecosystem level, are indicated by p values; n.s. when p > 0.05, * when 0.05 > p > 0.01, ** when 0.01 > p > 0.001, *** when p < 0.001. Sites that share a letter (*a* or *b*) share similar soil properties.

	BD (g/cm^3)	**Moisture (%)**	**TOC (%)**	**pH**	**EC (dS/m)**	**eCEC (c.mol/kg)**	**Na (mg/kg)**	**Nitrate N (mg/kg)**	**Total N (%)**	**K (mg/kg)**	**Ca:Mg (%)**	**$CaCO_3$ (%)**
0 - 10 cm												
Woodland	1.62 ± 0.09	1.7 ± 0.9	0.49 ± 0.14	7.6 ± 0.1 *a*	0.13 ± 0.03	14.7 ± 3.2 *a*	44 ± 6	11.6 ± 3.1	0.06 ± 0.01	342 ± 41	5.57 ± 1.26	2.4 ± 1.4
Shrubland	1.56 ± 0.08	1.2 ± 0.1	0.48 ± 0.04	7.9 ± 0.1 *ab*	0.12 ± 0.01	20.7 ± 2.3 *ab*	65 ± 25	13.8 ± 0.6	0.11 ± 0.01	496 ± 45	8.07 ± 1.62	2.9 ± 1.1
Mine path	1.58 ± 0.03	1.5 ± 0.4	0.53 ± 0.16	8.0 ± 0.1 *ab*	0.33 ± 0.05	29.9 ± 1.76 *b*	752 ± 378	22.3 ± 3.8	0.04 ± 0	317 ± 52	8.03 ± 1.84	5.1 ± 2.5
Overburden	1.8 ± 0.06	1.7 ± 0.6	0.22 ± 0.06	8.0 ± 0.03 *b*	0.27 ± 0.12	20.2 ± 1.3 *ab*	510 ± 367	22.8 ± 7.8	0.08 ± 0.01	473 ± 102	11.18 ± 2.36	2.9 ± 1.5
Soil stockpile	1.57 ± 0.08	1.8 ± 0.4	0.42 ± 0.11	8.0 ± 0.1 *ab*	0.23 ± 0.04	27.7 ± 0.9 *ab*	362 ± 137	17.7 ± 2.8	0.04 ± 0.01	287 ± 26	8.61 ± 1.9	11.3 ± 1.9
ANOVA												
Site level	n.s.	n.s.	n.s.	*	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Ecosystem level	n.s.	n.s.	n.s.	*	*	n.s.	*	*	n.s.	n.s.	n.s.	n.s.
10 - 20 cm												
Woodland	1.63 ± 0.06 *ab*	1.3 ± 0.2	0.52 ± 0.1 *a*	7.76 ± 0.09 *a*	0.11 ± 0.01 *a*	16.17 ± 4.09	88 ± 23	11 ± 2.7	0.05 ± 0.013 *ab*	260 ± 28	6.76 ± 1.67	3 ± 2.3 *a*
Shrubland	1.52 ± 0.02 *ab*	2.5 ± 0.5	0.29 ± 0.09 *ab*	7.97 ± 0.04 *ab*	0.12 ± 0.01 *ab*	24.62 ± 1.46	947 ± 518	13 ± 0.6	0.1 ± 0.007 *a*	330 ± 73	8.51 ± 1.95	7.8 ± 2.3 *ab*
Mine path	1.81 ± 0.13 *ab*	2.6 ± 0.1	0.31 ± 0.02 *ab*	8.1 ± 0.08 *ab*	0.36 ± 0.05 *b*	29.96 ± 0.89	1308 ± 478	17.7 ± 1.3	0.03 ± 0.003 *b*	257 ± 13	6.27 ± 0.82	11 ± 0.6 *ab*
Overburden	1.97 ± 0.14 *a*	1.3 ± 0.4	0.05 ± 0.01 *b*	8.12 ± 0.03 *b*	0.16 ± 0.04 *ab*	20.27 ± 0.61	558 ± 471	13.5 ± 2.3	0.08 ± 0.003 *ab*	333 ± 20	9.06 ± 0.83	2.3 ± 1.4 *ab*
Soil stockpile	1.31 ± 0.04 *b*	3.5 ± 1.5	0.86 ± 0.27 *a*	8.07 ± 0.06 *ab*	0.29 ± 0.02 *ab*	28.7 ± 1.58	832 ± 312	24 ± 11.1	0.05 ± 0.006 *ab*	197 ± 54	6.27 ± 2.11	20 ± 1.7 *b*
ANOVA												
Site level	**	n.s.	*	*	*	n.s.	n.s.	n.s.	*	n.s.	n.s.	*
Ecosystem level	**	n.s.	*	**	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Table continued.

	BD (g/cm^3)	**Moisture (%)**	**TOC (%)**	**pH**	**EC (dS/m)**	**eCEC (c.mol/kg)**	**Na (mg/kg)**	**Nitrate N (mg/kg)**	**Total N (%)**	**K (mg/kg)**	**Ca:Mg (%)**	**$CaCO_3$ (%)**
25 - 45 cm												
Woodland	1.53 ± 0.07	3.1 ± 1	0.21 ± 0.05	7.94 ± 0.22	0.18 ± 0.08 *a*	21.89 ± 2.18 *a*	236 ± 107	9.3 ± 0.9	0.04 ± 0.014	191 ± 47	6.31 ± 1.81	5.8 ± 3.5
Shrubland	1.59 ± 0.07	3.2 ± 0.7	0.33 ± 0.13	8.17 ± 0.08	0.24 ± 0.08 *ab*	26.86 ± 1.74 *ab*	1034 ± 389	11.8 ± 0.4	0.08 ± 0.002	220 ± 56	4.59 ± 0.65	14.4 ± 4.7
Mine path	1.7 ± 0.1	5 ± 1	0.62 ± 0.29	8.32 ± 0.01	1.07 ± 0.12 *b*	36.27 ± 0.97 *b*	1464 ± 468	46 ± 13.6	0.03 ± 0	173 ± 19	3.06 ± 0.16	20 ± 4.5
Overburden	1.63 ± 0.14	3.4 ± 0.5	0.23 ± 0.11	8.11 ± 0.07	0.56 ± 0.28 *ab*	24.44 ± 3.08 ab	563 ± 302	13.5 ± 3.0	0.08 ± 0.005	295 ± 39	5.6 ± 1.35	6.7 ± 4.1
Soil stockpile	1.58 ± 0.06	2.8 ± 0.2	0.82 ± 0.35	8.1 ± 0.05	0.47 ± 0.17 *ab*	27.98 ± 0.76 ab	210 ± 41	48.9 ± 20.2	0.04 ± 0.007	83 ± 39	5.48 ± 1.14	27.7 ± 5.5
ANOVA												
Site level	n.s.	n.s.	n.s.	n.s.	*	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Ecosystem level	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
55 - 75 cm												
Woodland	1.57 ± 0.05	4 ± 0.8	0.24 ± 0.09	8.27 ± 0.06	0.52 ± 0.18	29.88 ± 1.29	749 ± 208	10.8 ± 1.2	0.04 ± 0.008	183 ± 46	4.42 ± 0.63	15.3 ± 5.5 *ab*
Shrubland	1.6 ± 0.06	3.8 ± 0.7	0.47 ± 0.12	8.33 ± 0.06	0.52 ± 0.24	28.14 ± 2.24	214 ± 130	11.4 ± 0.2	0.07 ± 0.002	194 ± 31	3.05 ± 0.32	22.8 ± 4 *ab*
Mine path	1.78 ± 0.08	4.7 ± 0.1	0.43 ± 0.29	8.39 ± 0.02	1.3 ± 0.15	38.18 ± 1.33	1021 ± 843	30.7 ± 6.5	0.03 ± 0	150 ± 20	2.64 ± 0.11	20.3 ± 3.7 *ab*
Overburden	1.54 ± 0.05	4.8 ± 0.8	0.07 ± 0.01	8.07 ± 0.08	1.79 ± 0.89	31.98 ± 8.1	964 ± 396	22.1 ± 7.8	0.07 ± 0.007	233 ± 37	5.48 ± 0.86	4.8 ± 1.3 *a*
Soil stockpile	1.58 ± 0.02	3.2 ± 0.4	0.58 ± 0.05	8.22 ± 0.16	0.82 ± 0.36	30.26 ± 1.55	282 ± 82	94.7 ± 50.9	0.04 ± 0.007	125 ± 28	4.52 ± 1.03	35 ± 8.7 *b*
ANOVA												
Site level	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*
Ecosystem level	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
85 - 105 cm												
Woodland	1.57 ± 0.06	4.8 ± 0.6	0.26 ± 0.16	8.38 ± 0.04	1.01 ± 0.26	29.12 ± 1.72	1181 ± 227	10.6 ± 1.1	0.04 ± 0.008	216 ± 37	3.02 ± 0.36	24.4 ± 4.3
Shrubland	1.53 ± 0.11	6.8 ± 2.7	0.24 ± 0.09	8.44 ± 0.12	0.92 ± 0.38	30.89 ± 3.6	302 ± 142	11.8 ± 0.2	0.06 ± 0.004	238 ± 25	2.38 ± 0.29	20.6 ± 5.2
Mine path	1.73 ± 0.24	4.4 ± 1.8	0.11 ± 0.03	8.27 ± 0.08	1.49 ± 0.52	27.95 ± 5.22	1410 ± 201	10.1 ± 0.5	0.03 ± 0	96 ± 28	3.93 ± 0.46	2 ± 0.8
Overburden	1.71 ± 0.05	4.1 ± 0.9	0.05 ± 0.01	7.68 ± 0.32	1.47 ± 0.52	18.88 ± 4.8	777 ± 327	9.3 ± 1.6	0.05 ± 0.009	142 ± 21	2.05 ± 0.57	2.3 ± 1.4
Soil stockpile	1.59 ± 0.04	5.8 ± 0.9	0.51 ± 0.31	8.34 ± 0.19	1.22 ± 0.53	35.74 ± 0.9	1488 ± 640	58.7 ± 28.6	0.04 ± 0.007	213 ± 28	3.02 ± 0.4	18.8 ± 6.2
ANOVA												
Site level	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Ecosystem level	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.	***

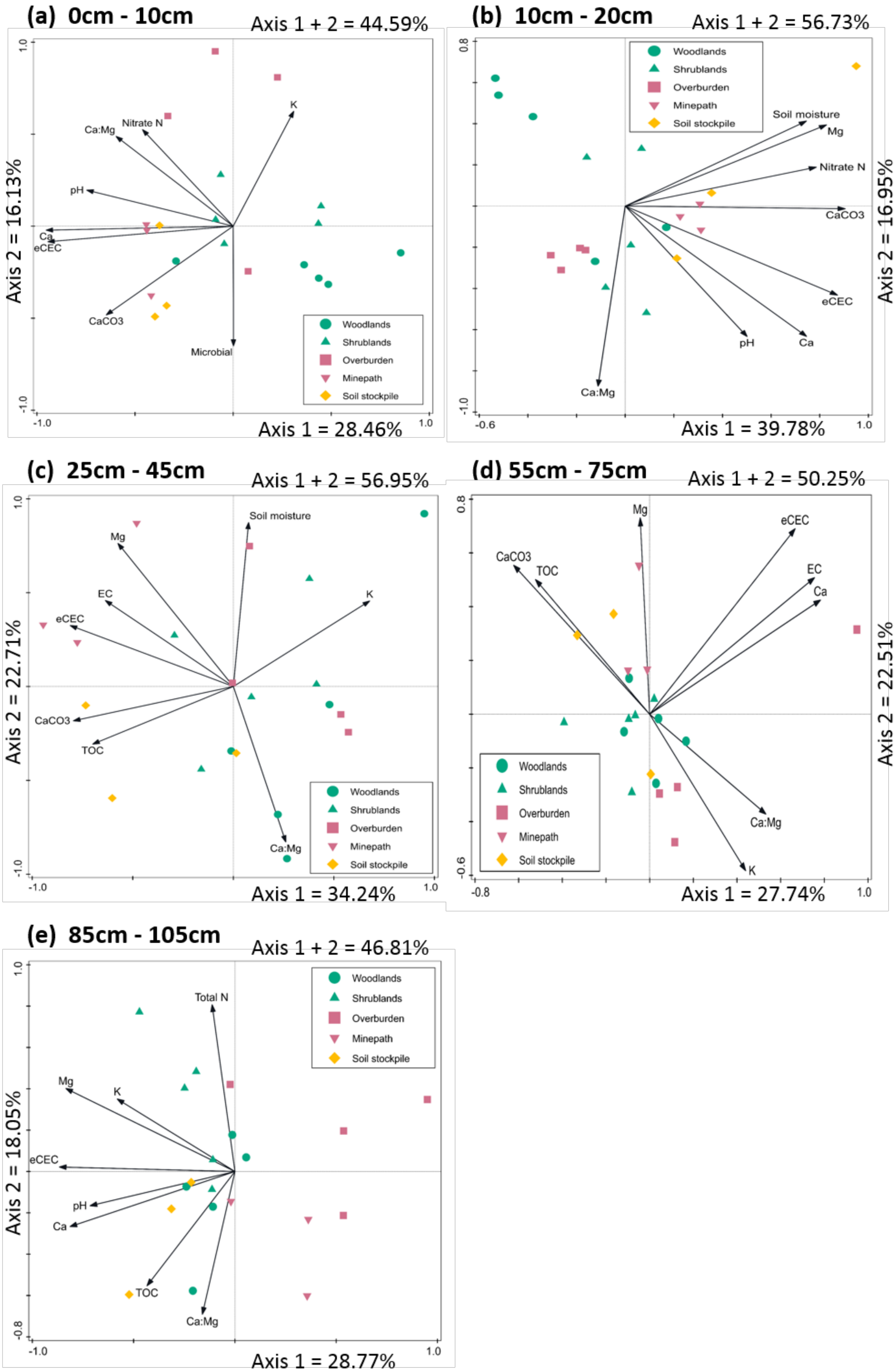

(a) 0cm - 10cm
Axis 1 + 2 = 44.59%
Axis 2 = 16.13%
Axis 1 = 28.46%
1.0
-1.0
-1.0
1.0
K
Nitrate N
Ca:Mg
pH
Ca
eCEC
CaCO3
Microbial
Woodlands
Shrublands
Overburden
Minepath
Soil stockpile
(b) 10cm - 20cm
Axis 1 + 2 = 56.73%
Axis 2 = 16.95%
Axis 1 = 39.78%
0.8
-1.0
-0.6
1.0
Woodlands
Shrublands
Overburden
Minepath
Soil stockpile
Soil moisture
Mg
Nitrate N
CaCO3
eCEC
pH
Ca
Ca:Mg
(c) 25cm - 45cm
Axis 1 + 2 = 56.95%
Axis 2 = 22.71%
Axis 1 = 34.24%
1.0
-1.0
-1.0
1.0
Soil moisture
Mg
EC
K
eCEC
CaCO3
TOC
Ca:Mg
Woodlands
Shrublands
Overburden
Minepath
Soil stockpile
(d) 55cm - 75cm
Axis 1 + 2 = 50.25%
Axis 2 = 22.51%
Axis 1 = 27.74%
0.8
-0.6
-0.8
1.0
Mg
eCEC
CaCO3
TOC
EC
Ca
Ca:Mg
K
Woodlands
Shrublands
Overburden
Minepath
Soil stockpile
(e) 85cm - 105cm
Axis 1 + 2 = 46.81%
Axis 2 = 18.05%
Axis 1 = 28.77%
1.0
-0.8
-1.0
1.0
Woodlands
Shrublands
Overburden
Minepath
Soil stockpile
Total N
Mg
K
eCEC
pH
Ca
TOC
Ca:Mg

Fig 4.6: Principal component analysis (PCA) ordination biplot for five soil depths (a-e) of the eight most important soil properties for explaining variation at each site. TOC = total organic carbon, EC = electrical conductivity, eCEC = effective cation exchange capacity, Nitrate N = nitrate nitrogen, Total N = total nitrogen, K = potassium, Ca = calcium, Mg = Magnesium, Ca:Mg = calcium to magnesium ratio and CaCO3 = calcium carbonate. Microbial activity (Microbial) was recorded in the 0cm – 10cm layer only (a).

4.4.4 Microbial activity

Microbial activity was greatest in shrubland soils, and remnant soils showed less variation in microbial activity between sites than rehabilitation sites (Fig 4.7a). There was a significant (*R* = 0.75, *p* = 0.021) and negative relationship with microbial activity and year since restoration (Fig 4.7b). Microbial activity was greatest at the oldest reconstructed site (the overburden site restored in 2009), however it was removed from the temporal analysis because it was the only site with soils inoculated with microbial activity prior to seeding. Amongst all other restoration sites, microbial activity progressively declined with time since restoration.

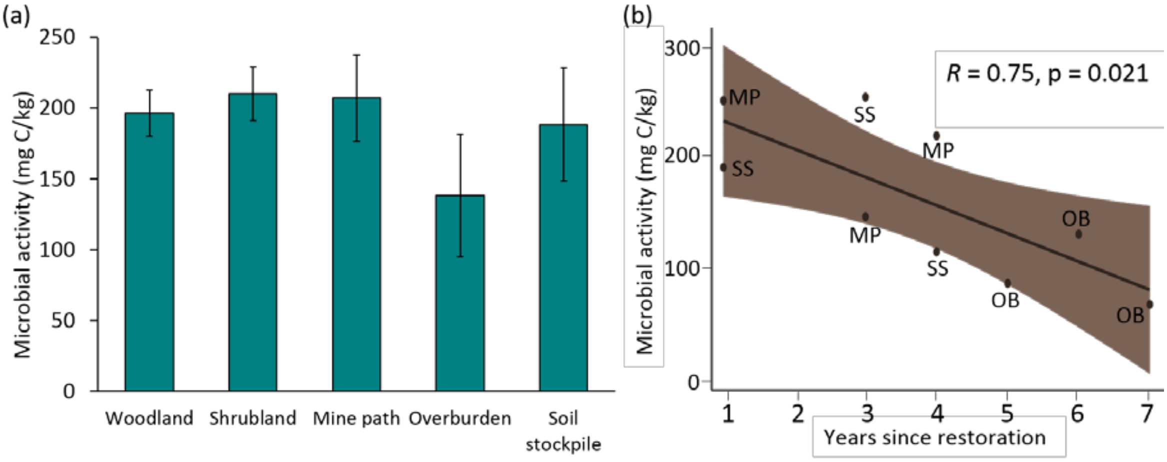


Fig 4.7: Microbial activity, or microbial biomass carbon, at study sites. (a) Mean microbial activity amongst ecosystems, with SE. (b) There was a significant correlation with microbial activity and year since restoration. Letters below points in correlation chart indicate restoration site: OB = overburden, MP = mine path and SS = soil stockpiles.

4.5 DISCUSSION

The aim of the study was to assess soil structure and properties in a remnant arid ecosystem, and to understand if reconstructed soil profiles after mining exhibit similar structure and properties to the remnant systems. Soils from the natural ecosystem exhibit two key physical characteristics that are beneficial for reducing evaporation from topsoil layers, and for preventing moisture loss to deep drainage, indicating resistance to water loss. Specifically, all remnant sites had topsoils that are course in texture, but as soil depth increases, clay content and compaction increased. Additionally, reconstructed soils differed from the remnant ecosystem in soil properties, particularly in the distribution of clay content and variables associated to the distribution of ions. These properties are crucial factors regulating soil hydrological function, root development and plant-water uptake (Cross et al. 2018; Huang et al. 2012b). Vegetation structure and soil properties in reconstructed sites were more similar to shrubland than woodland sites which, in this ecosystem, may be due to feedback effects of leaf litter from shrubs (Qu et al. 2016; Yao et al. 2019) and reduced competition from a lack of tree and grass species (Pierce et al. 2019).

4.5.1 Soil structure and water movement in remnant arid ecosystems

Soils in remnant sites were characterised by course-textured topsoils and fine-textured subsoils at maximum root zone depths. This soil structure enhances infiltration and reduces moister evaporation from the surface (Noy-Meir 1973), whereas increased clay content at lower horizons has been reported to prevent water leeching to depths beyond active root zones (Sala et al. 1988). This specific arrangement of particle-size distribution is likely critical to plant productivity in this arid ecosystem, where evaporation exceeds rainfall across all months. As most rainfall events reported in the study system are typically < 10 mm (Environdata 2019), ecosystems commonly experience water deficit, particularly during hot summer periods. Thus, increasing infiltration in the topsoil (by increasing sand/organic matter content), while preventing water loss to deep drainage by high clay content at depths below maximum root zones is beneficial in this system, because all plant species in this ecosystem are generally shallow rooted. Future studies should test these dynamics on plant growth under controlled glasshouse conditions, and field conditions, to understand plant-soil interactions to greater detail than investigated here.

Higher sand content in upper soil layers in arid zones is also linked to more stable soil-moisture dynamics (Zhang and Shao 2013). Remnant soils had higher surface compaction than expected, which may increase evaporative water loss from the compacted soil surface and inhibit seedling establishment (Fan et al. 2018a; Nawaz et al. 2013; Uselman et al. 2015). Higher surface compaction in remnant soils may represent degradation from drought, the trampling effects from wildlife or, conversely, natural hydrological processes of surface soils to enhance water run-off towards vegetated patches (Tongway and Ludwig 1990). Physical, chemical and biological crusts can influence surface compaction and subsequent hydrological processes, and are necessary to reduce soil erosion and facilitate water flows (Eldridge et al. 2002; Kidron 2014). Crust formation has been linked to soil-water retention and repellence, however the role crusts play in controlling soil-moisture dynamics is complex, and warrants further studies (Belnap et al. 2006; Gypser et al. 2016).

4.5.2 Soil reconstruction affects the distribution of properties for plants

Soil properties in the reconstructed system tended to differ to soils from remnant sites. In general, soil reconstruction increased bulk density at 10 – 20cm depths, to levels considerably higher than observed in healthy remnant soils. Bulk density of productive natural soils generally range from 1.1 to 1.5 g/cm^3, and values greater than this directly limit plant growth as most species are unable to grow roots effectively through high bulk density soils (Sheoran et al. 2010; Singh et al. 2015). For sandy clay loam soils, bulk density is approximately > 1.75 g/cm^3, and conditions for plant function are not optimal (Arshad et al. 1996; Schoonover and Crim 2015). Increased bulk density at reconstructed sites at 10 – 20 cm will increase evaporative water loss and erosion potential of soils. These effects will inevitably have negative impacts on establishment of woodland species (Heras 2009; Lindemann et al. 1984; Sheoran et al. 2010). High bulk density in soils is commonly associated with disturbance and increased likelihood of desertification (Huang et al. 2007; Su et al. 2004; Zhengha et al. 2004), which are common problems affecting vegetation recovery in post-mining restoration efforts (Shrestha and Lal 2011; Sinnett et al. 2008).

Sites containing reconstructed soils appeared to lack a deep clay layer that is integral to reducing drainage in arid regions. Additionally, reconstructed soil had high sand content at depths below 85 cm. The role and importance of a clay layer in capping water loss to deep drainage in arid regions is widely recognised (Eamus et al. 2013; Fayer and Gee 2006), and there is strong evidence that a clay layer at lower root zone depths strongly influences plant productivity (Macinnis et al. 2010; Zeppel et al. 2008). Other important ecosystem components that reduce deep drainage include vegetation cover and plant roots (Scanlon et al. 2005), and hence recently reconstructed soils with little vegetation structure are likely further prone to water loss from deep drainage. Many woody species in the arid zone rely on large rainfall events to recruit and grow (Wiegand et al. 2004), therefore the understanding fate of water following large rainfall events is important. High sand content at depths below 85 cm may effectively reduce the ecological impact of large rainfall events, and is potentially a critical factor contributing to water loss in reconstructed soils at the study site. The loss of profile due to mixing of soil horizons, and subsequent decrease in soil-moisture retention, are considered key soil attributes limiting plant function and establishment at the study site.

Reconstructed soils had different chemical properties to remnant soils and these differences may impact the soil-water balance and plant soil interactions (Sheoran et al. 2010). Soil pH in reconstructed soils in this study were slightly alkaline (pH = 8.0 – 8.4) at nearly all depths, because little leaching and high evaporation causes ions to concentrate in the soil (Hall et al. 2009). These thresholds are known to impede plant growth (Kopittke and Menzies 2004; McCauley et al. 2017), with most plants species favouring lower ranges (pH = 5.5 – 8.0) (Gazey 2018). At soil pH above 8.5, previous studies have reported soil structure degradation, reduced infiltration rates and decreased plant productivity (McCauley et al. 2017). These characteristics are likely impacting on the restoration performance in the study site, and further research should investigate ecophysiological performance of establishing plants more intensively. The high soil pH thresholds at reconstructed sites are likely caused by topsoil losses at all stages of soil movement around the mine. This includes initial topsoil-stripping, storage and redistribution onto rehabilitation surfaces. Topsoils are particularly susceptible to mixing with higher-pH subsoils during initial topsoil stripping prior to mining activities. Similar increases in pH and electrical conductivity were observed after mining in sites in Northeast America (Shrestha and Lal 2011), and in the arid regions of China (Huang et al. 2018) and Western Australia (Cross et al. 2018), causing poor hydraulic conductivity and inhibiting plant growth (Seybold et al. 2004).

Microbial activity declined with restoration age in this study, which was not what we expected. We expected low microbial activity immediately after soil reconstruction, because when topsoil layers are removed and stockpiled during mining operations, microbial communities are buried underneath upper soil layers (Sheoran et al. 2010), which can limit soil aeration and induce anaerobic conditions (Ghose 2001). However, most studies report biocrusts slowly recovering during the first 15 years of restoration (Hou et al. 2018; Li et al. 2018; Xiao et al. 2019; Zhang et al. 2016), although successional times are likely species-specific (Banning et al. 2011) and dependent on soil quality (Nautiyal et al. 2010). As the age of the restoration sites increases, plant biomass and subsequent leaf litter generally increases on the soil surface. Thus, increased soil health and microbial activity are expected of late-reconstructed soils (Orozco-Aceves et al. 2017). Soil-moisture and nutrient content (Chandler et al. 2019), clay content (Sessitsch et al. 2001) and particularly soil pH (Lauber et al. 2009; Rousk et al. 2010), are the primary factors affecting growth of biocrusts. Considering reconstructed soils have course soils at depths below 85 cm, and higher pH and salinity, these soil properties are likely key reasons explaining poor microbial responses to time since restoration. Certainly, high soil moisture content by reducing runoff and increasing infiltration has been shown to facilitate the growth and restoration of important cyanobacterial crusts (Bu et al. 2014), which are dominant phyla across the study region (Chilton et al. 2015; Eldridge and Greene 1994; Schultz et al. 2015). Despite the negative correlation with microbial activity and time since restoration, the oldest overburden site (which was removed from the temporal analysis as it was the only site with biocrust inoculates added to soils during reconstruction) had the highest microbial activity and this may be evidenced to the long-term benefits to treating reconstructed soils with microbial inoculates (Muñoz-Rojas et al. 2018; Wang et al. 2009; Williams et al. 2015).

4.5.3 Implications for management

Disturbance through mining causes anomalies in soil properties and specifically, increases soil bulk density, compaction, pH and variables associated with salts, and reduces microbial activity. These soil properties directly affect water availability and plant-water uptake, and are key barriers to arid ecosystem restoration. Restoration efforts should focus on reducing compaction and bulk density of soils near the surface, to reduce evaporative water loss and improve soil quality and plant health. Recovery of compacted soils in arid zones has been reported to be incredibly slow. Compaction recovery from mining in the Great Basin Desert took 100 – 130 years to recover (Knapp 1992). Similarly, soil compaction from military exercises in the Mojave desert required 70 – 140 years to recover (Webb et al. 1986; Webb 2002). Methods to minimise heavy tractor use should be considered in future arid restoration project, to reduce bulk density and evaporative water loss from surface layers. Reducing surface compaction and bulk density can be achieved using amendments of coarsely-ground organic matter (Sheoran et al. 2010), which should also enhance some microbial communities (Mengual et al. 2014). However, microorganisms have varied responses to soil amendments, and some taxa exhibit significant positive changes with amendments of water and organic matter, while other taxa decline (Buelow et al. 2016). Prior to introducing large quantities of foreign organic fractions to impoverished soils, field experiments should be conducted to understand the decomposition rates of soils with organic amendments, plant responses to increased organic matter, microbial taxa present and their response to temperature and water availability. The degradation of arid soils through salinization, desertification, contamination (Krasilnikov et al. 2016; yaşar Korkanç and Korkanç 2016) and loss of soil structure (Baumgartl and Horn 1991) is occurring at increasing rates and considered key threatening processes to arid ecosystems under climate change (Plaza et al. 2018). Reclamation of severely disturbed arid zones can be managed more effectively when the biophysico-chemical properties of soils have been assessed, and methods to ameliorate conditions unfavourable for plant growth are considered in restoration programs.

CHAPTER 5

RECONSTRUCTED SOILS HAVE A LOWER SOIL-MOISTURE RESPONSE THAN REMNANT SYSTEMS AFTER RAINFALL EVENTS

5.1 ABSTRACT

Aims: Rainfall in arid environments drive community dynamics, and typically falls in small and infrequent events. Despite recent theoretical advances in our understanding of the temporal link between rainfall, soil moisture and ecological feedbacks, we still lack quantitative assessments of soil moisture responses to rainfall events in natural arid ecosystems. The key aim of this research is to understand how rainfall events translate to soil moisture and ecosystem functioning in arid ecosystems, including those in their remnant state, and those that have been reconstructed after mining.

Methods: I installed four soil-moisture monitoring probes, with five sensors at depths to 90 cm, in arid woodland and shrubland sites, and monitored soil moisture hourly for over one year. Two additional soil-moisture probes were installed and monitored at sites with reconstructed soil profiles after disturbance from mining.

Results: Small rainfall events (< 10 mm) were most common, but did not affect soil moisture at depths below 5 cm. Large rainfall events > 20 mm were not recorded during this study, and no changes in soil moisture at depths below 15 cm were recorded in response to any rainfall event. The reconstructed soils had lower rainfall infiltration and retention at 15 cm than remnant soils, which suggest increased evaporation and/or run-off from surface layers.

Conclusions: This study provides unique and quantitative insights into the complex relationship between soil moisture and the different types of rainfall events commonly observed in arid zones. This research improves our understanding of how rainfall events in arid zones translate to soil moisture, and highlights the importance of incorporating methods to reduce evaporative water loss in arid soils reconstructed after mining.

5.2 INTRODUCTION

Rainfall in arid ecosystems is strongly linked to plant productivity (Noy-Meir 1973; Sala et al. 1988) and the distribution patterns of vegetation is regulated by complex climate–soil–vegetation dynamics (Porporato et al. 2002). The importance of spatial variability of soil moisture in arid ecosystems has long been recognised, but there remains gaps in our understanding and identification of factors that control the spatial and temporal variability in soil moisture (Pan and Wang 2009). Due to the high costs and logistical challenges associated to quantifying soil properties at different scales (Seyfried 1998), few studies have assessed real-time soil-moisture dynamics in natural, arid ecosystems. Most studies are confined to agricultural regions, or use remote sensing technologies that are restricted to near-surface assessments only, to depths of 5 cm (Santanello et al. 2007). Very few studies report on soil moisture within the soil profile in real-time (Pan et al. 2015), and we require a greater understanding of soil moisture dynamics at depths important for plant uptake. Surface moisture is tightly linked with levels of microbial activity (Lucas et al. 2008), which is an important source of carbon and productivity in arid zones (Agarwal et al. 2014). Soil moisture in arid ecosystems largely determines the community organisation and carrying capacity for vegetation (Rodriguez-Iturbe et al. 1999), hence understanding soil moisture dynamics in response to climatic fluctuations is crucial for plant conservation and restoration.

Rainfall in arid environments typically falls in small and infrequent events (Ogle and Reynolds, 2004). Arid regions generally receive < 15 rain events per year, although less than six are sufficiently large to affect biotic parts of the ecosystem, thus rainfall is short in duration relative to the periods of no rainfall between them (Noy-Meir 1973). Most rainfall events in deserts are very small, with more than 85 percent of events less than 5 mm (Sala et al. 1988). The effects of precipitation events are difficult to generalise because soil moisture is dictated by temperature and the temporal distribution of rainfall, as well as an array of complex ecological factors and soil properties. Theory suggests that all arid soils are generally dry in the upper 5 or 10 cm within 5 - 25 days of wetting, but it takes many weeks for the 10 – 30 cm layer to dry out, and for many months longer there is little evaporative loss from the soil below 30 cm (Noy-Meir 1973). Higher evaporation rates in summer than winter mean that summer rains are considered less effective, or less biologically meaningful, than winter rains. However, due to the lack of studies that assess real-time soil moisture dynamics and rainfall in arid zones, we still lack a solid understanding of the temporal link between rainfall, soil moisture and feedbacks to the environment (Bardgett et al. 2005; Ogle et al. 2014; Reynolds et al. 2004).

The spatial and temporal response of soils to rainfall vary at different scales (Schneider et al. 2008), and is influenced by the initial soil moisture conditions (Famiglietti et al. 1998). Soils can store moisture for long periods, which is described as a ‘memory’ of past precipitation events and anthropogenic disturbances (Schwinning et al. 2004), because the initial soil moisture level influences the response of soil to new rainfall events. Thus soil ‘memory’ makes it difficult to generalise responses to moisture input. Multiple precipitation events may be additive when the time between pulses is short, but this effect decreases as the number of between-event dry days increases (Loik et al. 2004). The effects of the first few pulses following extended drought may have no biological impact. We require better knowledge about the mechanisms relating ecological responses to rainfall timing to generate general principles about the effects of rainfall in this ecosystem, and to understand the differences between difference arid zones (Ogle et al. 2014). Climate change is expected to cause changes in the timing, duration and magnitude of precipitation events, which can induce significant changes in ecosystem function and community structure (Schwinning and Sala 2004). A major concern during the past years has been the identification of factors controlling spatial and temporal soil moisture variability (Grayson et al. 1997; Schneider et al. 2008) and the quantification of changes in soil moisture at different scales (Brocca et al. 2010; Seyfried 1998; Skøien et al. 2003).

The sources of water availability in arid ecosystems are often ignored, and not only confined to rainfall. In the absence of precipitation, the three main mechanisms by which water may be added to the uppermost soil surface is by fog deposition, dew formation, and adsorption of water vapour (Agam and Berliner 2006). During rain-free periods, air spaces within surface soils are dryer than the atmosphere, causing moisture to adhere to surface soil particles, thus atmospheric moisture may significantly contribute to soil-moisture content and constitute an important link in the water cycle of arid and semiarid regions (Kosmas et al. 1998; Kosmas et al. 2001; McHugh et al. 2015). Over extended periods without rainfall, water vapour adsorption is generally the only possible mechanism for moisture uptake by the soil, particularly in arid zones where the temperature of soil surfaces rarely drops below the dew point (Agam and Berliner 2006). Adsorption by soils involves a diurnal cycle of latent-heat flux, which is the heat transferred between soil surfaces and the atmosphere via moisture evaporation or condensation. Latent-heat flux generally increases with clay content of the soil, however, whether this phenomenon occurs in response to precipitation events only, in which case there would be no latent-heat flux during the dry season, is highly contentious (Agam and Berliner

2006). While the amount of moisture in soils from adsorption may not be directly available to plants, it may be critical in influencing the initial soil moisture conditions and hence moisture availability following rainfall (D'Odorico and Porporato 2004). Low temperatures enable the movement of water vapour from air to soil, and the subsequent increase in soil moisture, in turn, stimulates soil CO_2 efflux rates by increasing microbial activity (McHugh et al. 2015). Further studies are required to understand the dynamics and importance of adsorption and latent-heat flux across seasons in arid zones when rainfall is absent.

The degradation of arid ecosystems is one of the key ecological issues of the twenty-first century (Sivakumar 2007). Anthropogenic disturbance in arid zones leads to soil destabilisation and dust mobilisation (Pointing and Belnap 2014), erosion of nutrient cycles (Evans and Belnap 1999), reduced abundance of indigenous species, and reduced ecosystem services for humans (Abella 2012). The recovery of hydrological cycles and species composition in these systems can take decades, or even centuries (Abella 2010), and the impacts of disturbances are more severe with increasing water stress (Chaturvedi et al. 2017). Arid zones are particularly susceptible to degradation, even after minor disturbance events, because conditions for natural plant recruitment are spatially and temporally irregular, which can create challenges for restoration and conservation (Svejcar and Kildisheva 2017). Disturbance can also reduce soil moisture by affecting infiltration and evaporation (Kimiti et al. 2017), although our understanding of how disturbance effects moisture dynamics throughout the soil profile is limited. Most arid-zone research has been conducted in the Americas and Europe, yet Australian arid zones have considerably greater variability in rainfall and lower soil fertility (Morton et al. 2011) and hence could provide valuable counterpoints and insights to soil-moisture dynamics under changes in land-use.

The key aim of this research is to understand how rainfall events in an arid zone translate to soil moisture. Specifically I test the following hypothesis: 1) short and intermittent rainfall events (< 10 mm) do not affect soil moisture at depths below 5 cm, 2) only long or heavy rainfall pulses effect soil moisture at greater depths, 3) the diurnal cycle of latent heat flux is observed through wet and dry seasons, and hence is not dependent on rainfall, and 4) reconstructed soil profiles have lower water holding and infiltration capacity than remnant soils. I test these hypotheses with soil-moisture monitoring probes at different site types. This is the first study to assess soil moisture in real-time in a natural arid ecosystems, and hence provides unique and quantitative insights into the complex relationship between soil moisture and rainfall events.

5.3 METHODS

5.3.1 Site description

The study was conducted at the Ginkgo Mine (see chapter four for a study site description). I defined a rainfall event as one that was continuous, until rainfall stopped for one hour or more, and rainfall events either side of no rainfall hours were considered as discrete rainfall events. I assessed soil moisture over one year for two common types of vegetation communities from the study site: shrubland communities dominated by *Maireana* shrubs, and woodland communities dominated by *Casuarina pauper*. I also included overburden sites with a reconstructed soil profile after mining, and that have been re-vegetated. Photographs of example sites are provided in Fig 5.1. Soils of the area are generally sandy clay loam in texture, and clay content within the A horizon ranges from 10–35% (chapter four).

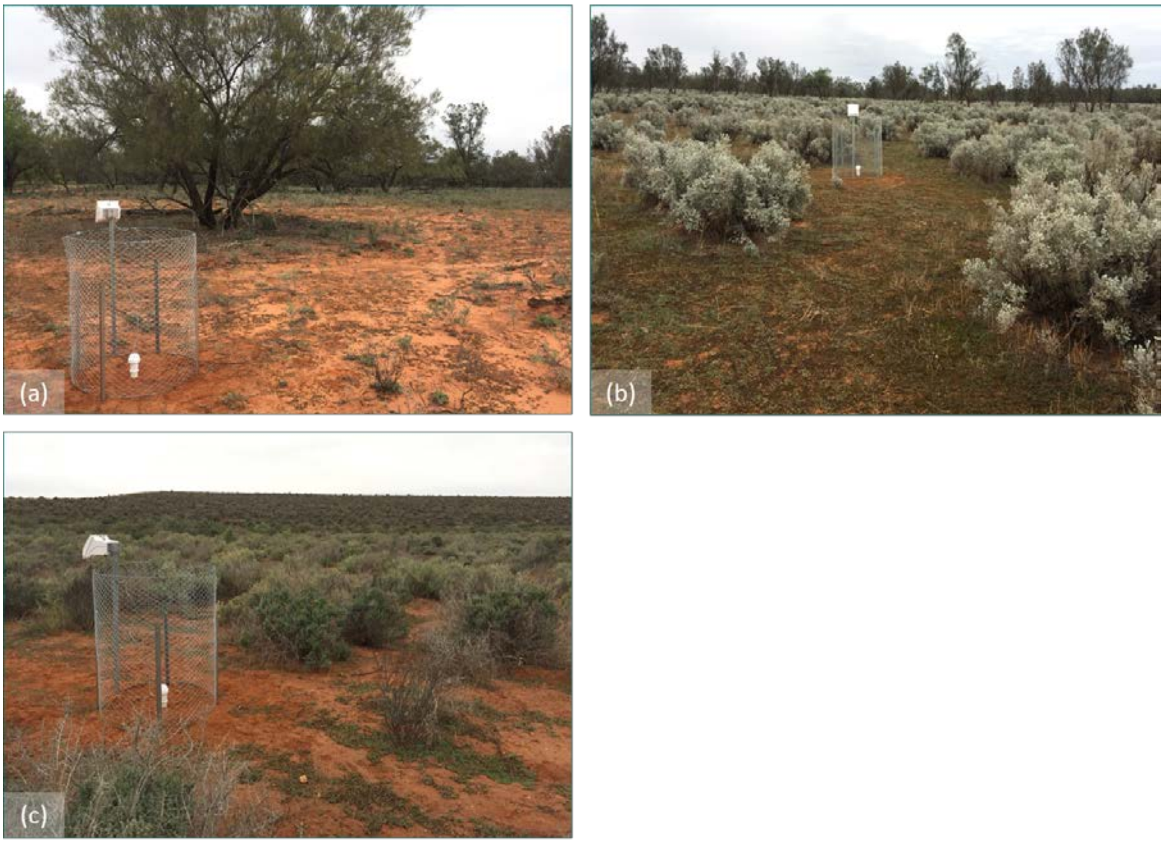


Fig 5.1: Installed soil-moisture monitoring probes at (a) a remnant woodland site, (b) a remnant shrubland site, and (c) an overburden restoration site that was reconstructed following sand mining.

5.3.2 Soil moisture monitoring

Soil moisture was assessed using six EnviroSCAN capacitance probes (Sentek Pty Ltd, Kent Town, South Australia). Each vegetation type (woodland, shrubland and revegetated overburden sites; Fig 5.1) had two soil-moisture monitoring probes installed which were separated by a distance of ~1.4 km. To install probes, a soil auger was used to excavate a hole that was slightly smaller in diameter than the access tube (Fig 5.2a), to a depth of 1.1 m. Each probe had one sensor placed at each of the following five depths: 5 cm, 15 cm, 35 cm, 65 cm and 95 cm depths. Each probe was housed inside a 56.5 mm diameter PVC access tube (Fig 5.2b), and sealed with a screw-top. The access tube was hammered into the excavated hole, ensuring no gap formation between the soil and the edges of the access tube. The bottom of the access tube was sealed using a specially designed bottom stopper to prevent underground moisture entering the tube. After installation, the inside of the access tube was cleaned and dried, the probe was placed inside and the screw cap was sealed closed with glue. Each probe was installed on bare soil, and at least 1 m from vegetation, and protected by a fence of 1.2 m diameter (Fig 5.2c). Probes were installed in May 2017, and left *in-situ* for over one year.

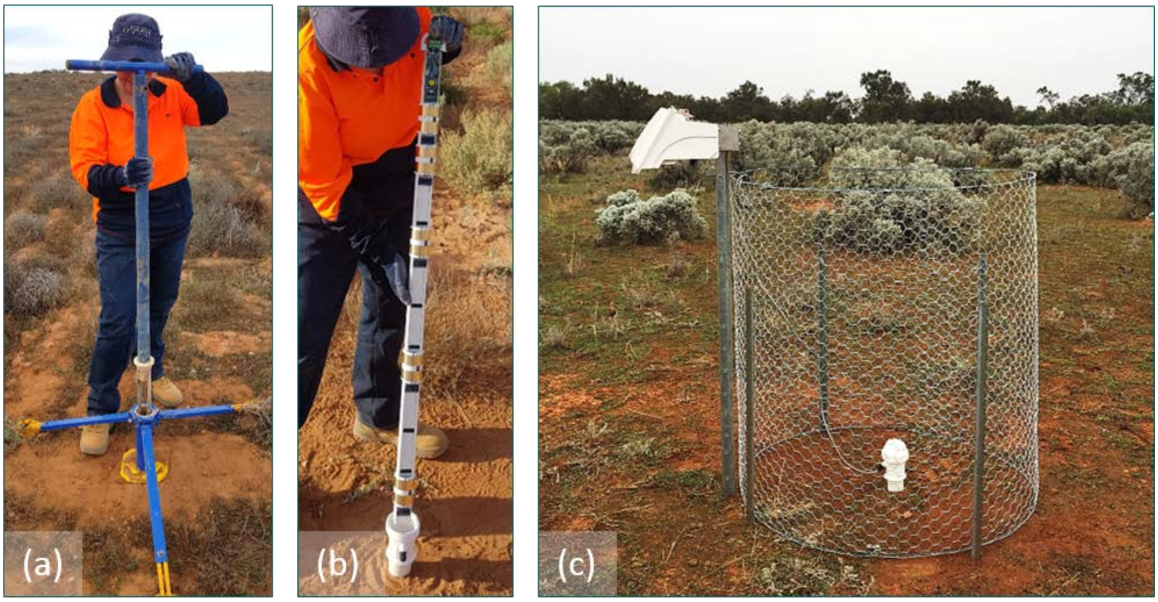


Fig 5.2: Installation of soil-moisture monitoring probes; (a) a soil auger used to excavate a hole (b) sensors on a probe, placed at 5 cm, 15 cm, 35 cm, 65 cm and 95 cm depths, to record soil moisture (c) Probes were fenced to prevent disturbance from kangaroos, goats, emus and rabbits.

Sensors were programmed to record moisture data at the start of every hour, and powered with a 6-volt lantern battery enclosed within a waterproof plastic housing. Every 2.5 months, soil moisture data was manually downloaded from sensors, batteries were changed, probes were checked for moisture infiltration, corrosion and dust, and encroaching weeds and grasses were removed. Each sensor was pre-normalised, and scaled in air and water inside the PVC pipe by Sentek Pty Ltd. Calibration of soil-moisture sensors was made by comparing scaled frequency readings, measured in the laboratory from within the access tube, with values of the volumetric water content. Volumetric water content was determined from pre-determined bulk density counts for sandy clay loam soils (Adelaide, South Australia, CSIRO). Normalisation counts used the following normalisation equation:

$$SF = (F_a - F_s) \div (F_a - F_w)$$

where SF is the scaled frequency, F_a is the raw air count in the PVC access tube while suspended in air, F_w is the raw water count in the PVC access tube in a water, and F_s is the raw field count in the PVC access tube in the soil at each particular depth level. The calibration equation (regression coefficient $R^2 = 0.974$) was applied after adjusting the normalised data using:

$$Y = 0.1957 \times X^{0.404} + 0.02852$$

Where Y is the scaled frequency, X is the volumetric soil-moisture content (%), and 0.1957, 0.404 and 0.02852 are the calibration coefficients A, B and C, respectively.

5.3.3 Data analysis

To understand differences in soil moisture between sites, I used t-tests for difference in means which was performed in R (R Core Team 2018) to generate *p* values for differences in soil moisture between sites following rainfall. Maximum increase in soil moisture from rainfall events, and time for soil moisture to decrease by 50% (from peak soil moisture after rainfall), was calculated in Microsoft Excel.

5.4 RESULTS

This study was conducted during one of the most persistent droughts in recorded history, hence rainfall was lower than expected. During this one-year experiment, total rainfall was 117 mm, over 56 rainfall events, but only two rainfall events were 10–15 mm (14.6 mm on the 11th of October, and 12.4 mm on the 1st of December, 2017). However, the 12.4 mm rainfall event in

December is considered the largest rainfall event during this study because it occurred closely within two smaller rainfall events (8.4 mm which fell eight hours earlier, and 9.2 mm which fell three hours later). Combined, these three rainfall events in December 2017, occurred over 35 hours and I present soil-moisture responses from these combined rainfall events in Figs 5.5 and 5.6. Of all rainfall events during this study, 88% were < 5 mm (Fig 5.3a) and short in duration. However, some of these small rainfall events (18%) lasted more than three hours (Fig 5.3b). There was no detectable effect on soil moisture at depths below 15 cm from any rainfall event during the study period.

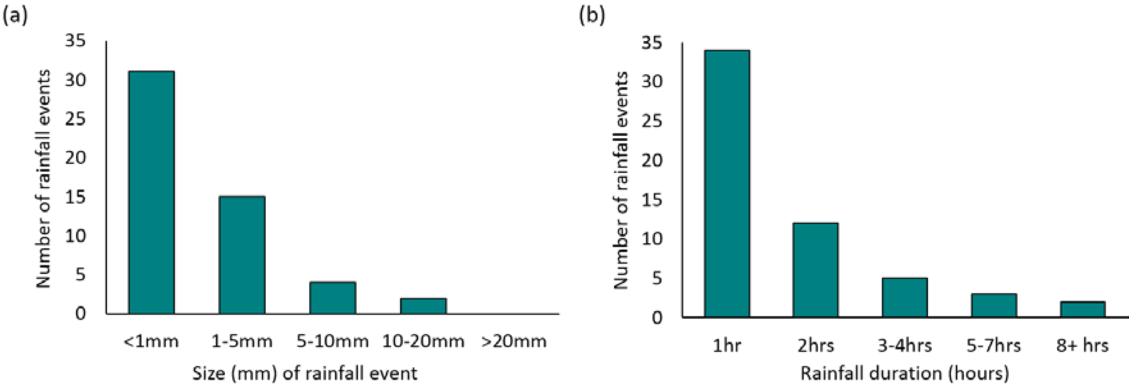


Fig 5.3: Rainfall events recorded at the study site during the study period (20/05/2017 – 21/05/2018), showing (a) the size of rainfall events, and (b) the duration of events (Environdata 2019).

5.4.1 Soil moisture from small rainfall events (< 10 mm)

Rainfall events < 10 mm had no detectable effect at wetting soil depths below the first sensor at 5 cm. Soil moisture content from rainfall events < 5 mm was similar across all sites, whereas woodlands were more responsive to rainfall events of 5–10 mm, and soil-moisture infiltration to 5 cm in the woodlands was considerably higher than observed at all other sites (Fig 5.4a). A 7.2 mm rainfall event in autumn caused soil moisture, at 5 cm, to increase by a maximum of 331 ± 92% at woodlands, but only 190 ± 3% at reconstructed sites. This pattern occurred across all seasons and likewise, a 9.0 mm rainfall event in summer caused soil-moisture content, at 5 cm, to increase by a maximum of 320 ± 71% at woodland, 137 ± 2% at shrubland and 120 ± 15% at reconstructed sites. Of these small rainfall events (presented in Fig 5.4a), soil moisture at 5 cm was significantly higher at woodlands than reconstructed sites following 5.4 mm in November (P = 0.041) and 8.2 mm in January (P = 0.048). Despite woodlands having greater moisture infiltration to 5 cm, moisture retention was greatest at shrublands (Fig 5.4b). A 7.2 mm rainfall event in autumn (May 2018) was retained for longer at 5 cm, than an 8.2 mm rainfall event during summer in January 2018 (Fig 5.4b), although there was no significant trend between moisture retention rates in winter and summer. However, a lack of rainfall events during this study impacted the ability to compare soil moisture responses to rainfall events of similar magnitude across different seasons.

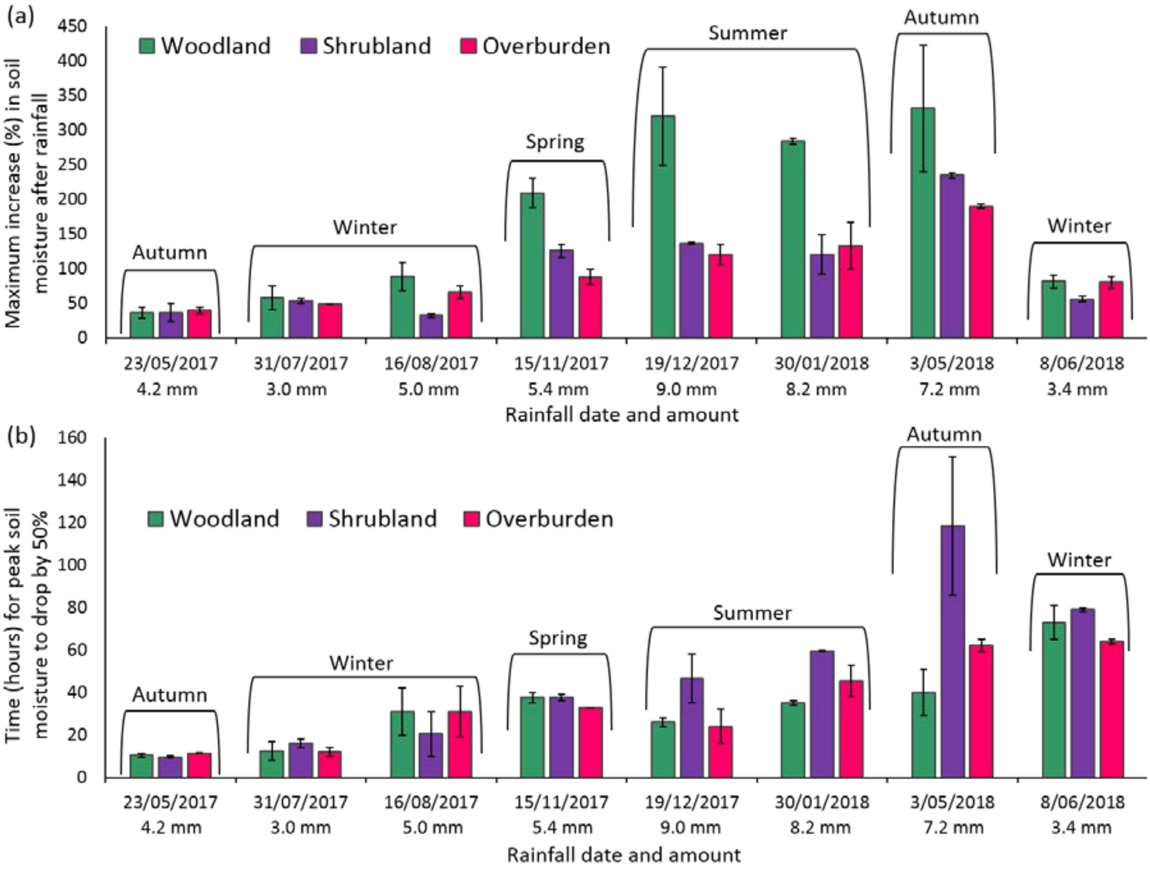


Fig 5.4: Soil moisture dynamics at 5 cm under small (< 10 mm) rainfall events. (a) Mean maximum increase (%) in soil moisture content following rainfall events. (b) Mean time (hours) required for peak soil moisture to decrease by 50% following rainfall. Magnitude (mm) and date of rainfall events are provided along the x axis, along with season of rainfall. Error bars represent SE (hours).

5.4.2 Soil moisture from large or subsequent rainfall events

Large rainfall events of > 20 mm, which generally occur a few times a year, were not recorded during this study. The largest, combined rainfall events occurred over 35 hours in summer (8.4 mm, 12.4 mm eight hours later, followed by no rainfall for three hours, and then 9.2 mm), and soil moisture responses from these combined rainfall events are presented in Figs 5.5 and 5.6. Soil moisture at 5 cm increased by a maximum of 350 ± 47% at woodlands, 327 ± 4% at shrublands and 354 ± 30% at overburden sites. Mean peak soil moisture at 5 cm occurred between 32 and 33 hours after rainfall for all sites (Fig 5.5a). Water infiltration to 5 cm occurred almost immediately after rainfall, but there was a lag time in soil moisture responses at 15 cm. The shape of soil moisture signatures from this largest rainfall event were markedly similar at 5 cm across all sites, but this was not the case at 15 cm. To give an indication of how long soil moisture persisted at each probe, I calculated the number of hours from the point of peak soil moisture after a rainfall event until the point when soil moisture had decreased by 50% of the peak value. This time was 58 ± 12 hours for woodlands, 137 ± 15 hours for shrublands, and 117 ± 18 hours for overburden sites.

Soil moisture at 15 cm was greatest at woodland sites and the effects of these combined, large rainfall events (8.4 mm, 12.4 mm and 9.2 mm, scattered over 35 hours, in December 2017), remained for up to one week following rainfall. However, by the next rainfall event (9 mm that occurred 19 days later) there was no memory at 15 cm of the previous large rainfall event. Overburden sites displayed soil moisture signatures more similar to shrublands than woodlands, in that they both exhibit only short-lived increases in soil moisture at 15 cm following rainfall events < 20 mm. Mean maximum increase in soil moisture at 15 cm, from the combined three rainfall events in summer (8.4 mm, 12.4 mm, and 9.2 mm) was 129 ± 18% at woodlands, 83 ± 15% at shrublands and 117 ± 12% rehabilitation sites (Fig 5.5b).

Soil moisture storage at 15 cm was highly variable at shrubland and overburden sites. For example, mean time for soil moisture to decrease by 50%, after the combined three rainfall events in December 2017 (Fig 5.5a), from peak soil moisture following rainfall, was 97.5 ± 15 hours at woodlands, 299 ± 117 hours at shrublands and 205 ± 98 hours at overburden sites. Soil moisture generally increased with depth in all three land-use types (Fig 5.5b) – i.e. the mean resting soil moisture was greater at 95 cm depth than at 65 cm, which was in turn generally (but marginally) greater than at 35 cm depth. Woodlands were the only sites to exhibit slight decrease in soil moisture content at 35 cm during the first 60 hours following rainfall (Fig 5.5c), which may be due to water uptake from plant roots. This is the sole occasion that soil moisture at depths ≥ 35 cm fluctuated in response to rainfall. Records of soil moisture responses to larger rainfall events than observed during this study are required to ascertain if these effects are due to plant-water use or capillary actions of soils with higher sand content in topsoils (as observed at woodland sites, see chapter four).

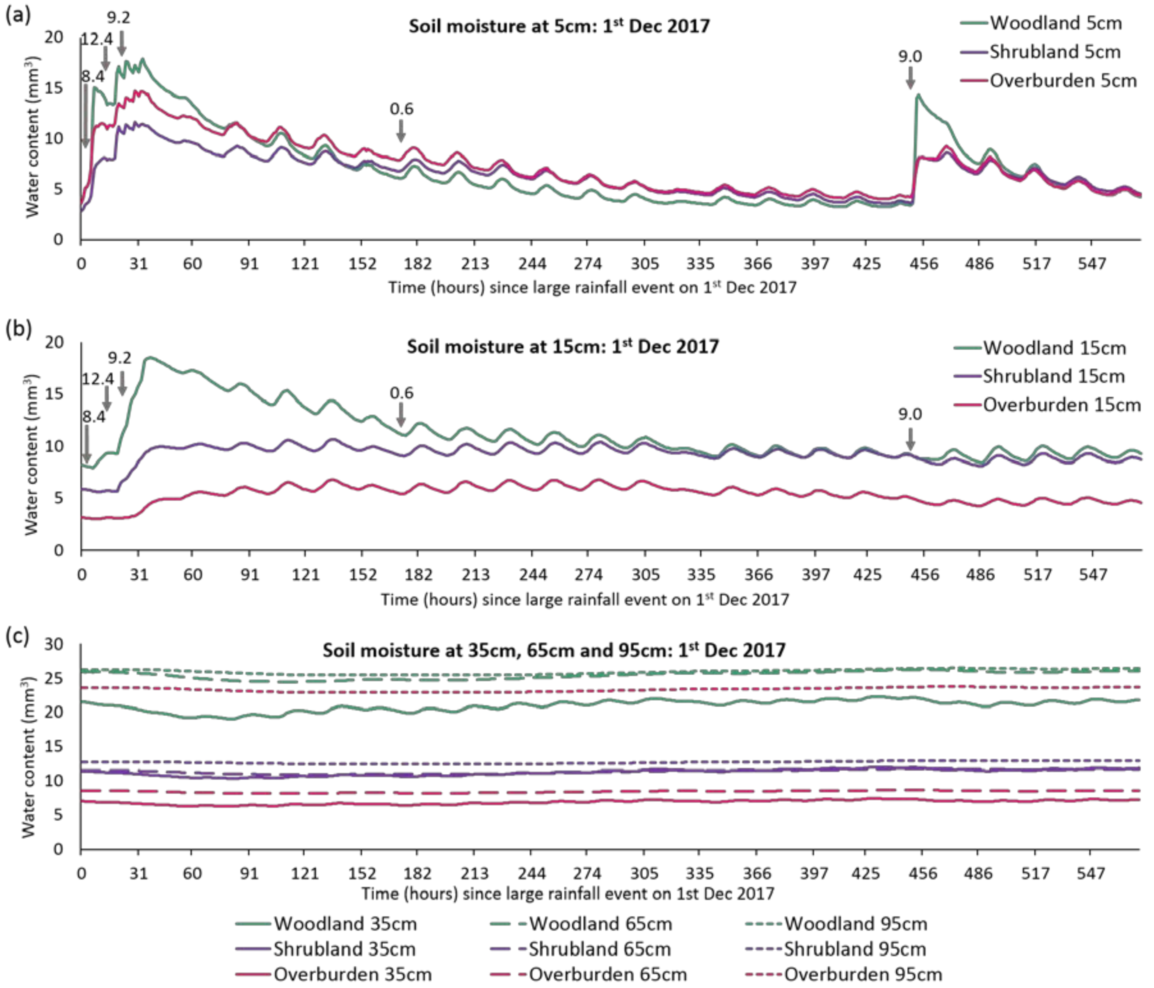


Fig 5.5: Soil-moisture signatures from the largest rainfall event observed during this study (includes three separate rainfall events, across 35 hours, that total 30 mm), and at different depths; (a) 5 cm, (b) 15 cm, and at (c) 35 cm, 65 cm and 95 cm. Rainfall amounts (mm) and time of rainfall arrival are displayed by numbers and arrows respectively, above charts (a) and (b). Errors bars have been removed for chart clarity.

At overburden sites only, soil moisture was always considerably lower at 15 cm than observed at 5 cm (Fig 5.6). Moisture infiltrated to 15 cm within 9 hours at woodland, within 20 hours at shrubland and within 32 hours at overburden sites and, furthermore, mean soil-water content at 15 cm exceeded soil moisture at 5 cm within 34 hours of rainfall at woodlands and within 47 hours at shrubland sites (Fig 5.6). At 24 hours following this large rainfall event, mean soil moisture content at 15 cm increased by 47 ± 9% at woodland, 13 ± 17% at shrubland and 0 ± 3% at overburden sites and furthermore, at 48 hours following rainfall, mean soil moisture content at 15 cm increased by 114.7 ± 12.8% at woodland, 57.0 ± 37.8% at shrubland and 53.7 ± 20.1% at overburden sites.

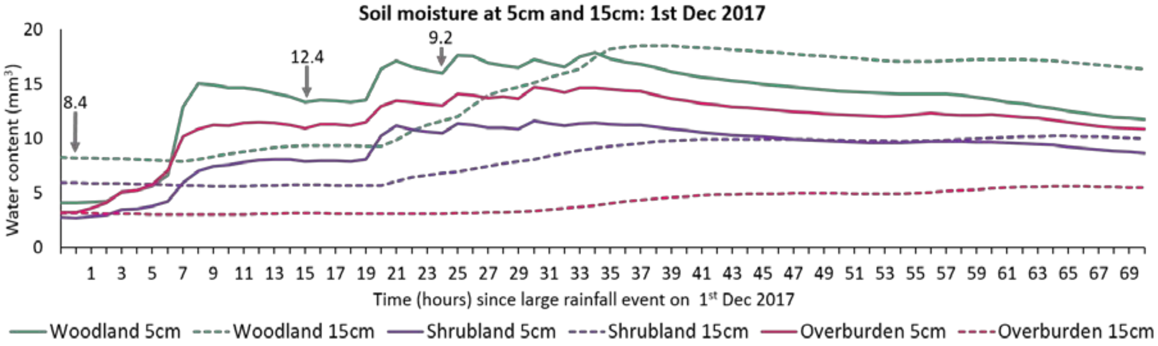
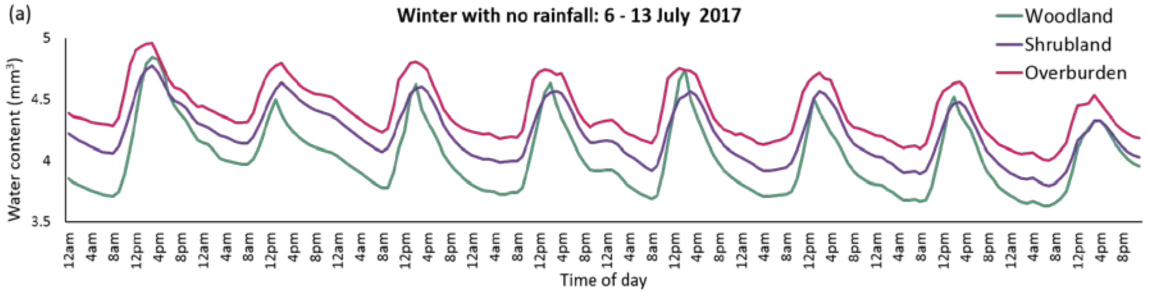


Fig 5.6: Soil-moisture responses from three separate rainfall events that were scattered across 35 hours and total 30 mm, and at two different depths; 5 cm (solid lines) and 15 cm (dotted lines). Rainfall amounts (mm) at the start time of rainfall arrival, are displayed by numbers and arrows above charts.

5.4.3 Diurnal cycle of latent-heat flux

Non-rainfall moisture inputs were observed at all seasons, including during long periods without rain, but only at upper depths of 5 cm and 15 cm. During dry periods in winter, diurnal-heat flux at 5 cm caused soil moisture to fluctuate by between ~10–30%, and this effect was greatest at woodland sites (Fig 5.7a). During summer periods of no rainfall, the impact of diurnal-heat flux on soil moisture content at 5 cm was greater during winter, and caused soil moisture to fluctuate by ~21% (Fig 5.7b). During rain-free periods, soil moisture content was lowest between 6:00 am – 8:00 am, and highest was between 1:00 pm – 3:00 pm, regardless of which season dry periods occur in.



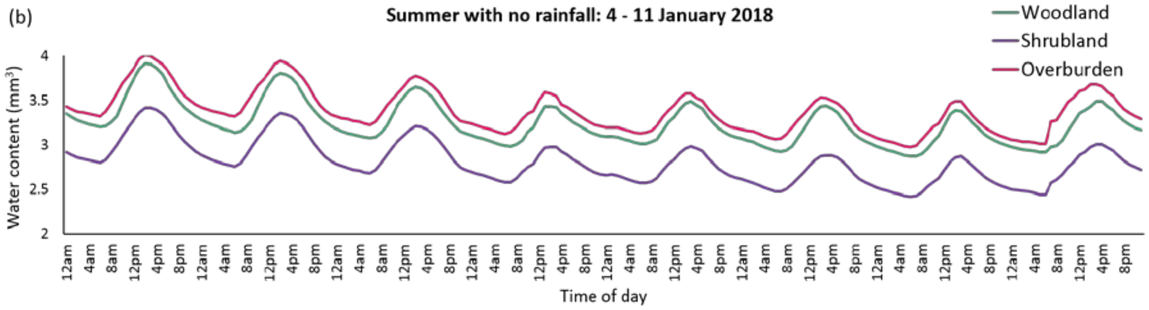


Fig 5.7: Diurnal changes in soil-moisture at 5 cm during extended, non-rainfall events. Diurnal heat-flux occurred daily and during extended dry periods, including (a) winter and (b) summer. Errors bars have been removed to improve legibility.

5.5 DISCUSSION

This research improves our understanding of how rainfall events in arid zones translate to soil moisture. Significant increases in soil moisture content occurred at the surface layer when rainfall was above 5 mm but, to impact soil moisture at 15 cm, larger rainfall events > 20 mm are required. This supports my first prediction, and findings from other arid zone studies, that show rainfall events < 10 mm, although most common, are generally ineffective at wetting soil depths below 5 cm (Noy-Meir 1973; Wei et al. 2008; Yu et al. 2015). In arid climates, and as observed in this study, the upper 5 cm - 10 cm are mostly dry within 5–25 days following rainfall, hence plants have little chance to extract water from this layer, and rainfall events under 5 mm will likely benefit only surface cryptogams and microbial communities (Noy-Meir 1973; Schwinning and Sala 2004). Certainly, the cumulative effect of small rainfall events < 10 mm on soil moisture was less than expected. Following the three rainfall events recorded here in December 2017, that were scattered across 35 hours and total 30 mm, soil moisture dropped to levels prior to rainfall within ~15 days, or 360 hours (Fig 5.5a). There was no evidence of plants extracting moisture from upper soil horizons following rainfall events < 30 mm.

5.5.1 Importance of rainfall events < 10 mm

Small rainfall events (< 10 mm) were most common, as predicted, but do not affect soil moisture at depths below 5 cm. As such, these events would be considered biologically insignificant for plants by Wiegand et al. (2004) and Veenendaal et al. (1996). Species from different lifeforms likely exhibit different physiological responses to water availably (Chesson et al. 2004; Schwinning and Sala 2004). Plants with traits which may benefit from small rainfall events, such as shallow-rooting C4 grasses, generally require smaller rainfall events to persist (Schwinning et al. 2003). Tree species tend to have deeper roots and hence require water at greater depths (Schenk and Jackson 2002). However, considering the similar rooting depths observed between shrub and tree species at the study site (chapter four), they are likely to respond to rainfall events similarly which may increase intraspecific competition for water when rainfall occurs (Shiponeni et al. 2011).

In response to large rainfall events, plant roots extract soil moisture causing a drop in the moisture signatures at rootzone depths (Sentek 2012). However, this pattern was not observed at any depth with rainfall events < 20 mm, which may suggest a lack of plant response to rainfall during this study. One key reason why plants in arid zones might not respond to rainfall is that rainfall amount may not be enough to cause a significant increase in soil moisture (Fernández 2007). Rainfall events of > 3 mm may elevate rates of carbon fixation in some higher plants

(Schwinning et al. 2003), and may enhance biological crusts (Belnap et al. 2004), although larger events are required to stimulate growth and productivity of trees and shrubs (López et al. 2008). Events of at least 20 mm may be required to trigger the germination of many desert plants (Beatley 1974; Veenendaal et al. 1996; Wilson and Witkowski 1998). Even though soil moisture responses were negligible at rainfall events < 5 mm, plants can still benefit from rainfall by taking up water through their leaves directly, or from the micro-environment humidity provided by small rainfall events (Wu et al. 2016). Another reason why plants may show no respond to rainfall events < 20 mm is because many arid species go into a dormant state during drought and do not take up water as readily as they would during normal rainfall conditions (Lesica and Crone 2007; Pnueli et al. 2002), considering this study was conducted during the most persistent drought in modern history. Certainly many arid species limit transpiration and water uptake when drought intensifies, leading to drought-enforced inactivity (Burgess 2006; Schwinning and Ehleringer 2001; van den Bilcke et al. 2013). To confirm the effects on soil moisture signatures from plant uptake, I suggest future studies that monitor soil moisture in vegetated and non-vegetated areas (that are otherwise similar).

5.5.2 Diurnal patterns of heat flux and evaporation

Arid ecosystems obtain water from sources other than rainfall, although little is known about the extent of soil moisture derived from atmospheric water vapour or its influence on arid species. Latent-heat flux refers to the amount of energy, or heat, transferred between soil surfaces and the atmosphere via moisture evaporation or condensation. Like most hot deserts, dew point temperatures at the study site are low and mean yearly dew point temperatures are 6°C - 7˚C (BOM 2019). As soil-surface temperature does not often drop below the dew-point temperature, dew occurs rarely, hence the clear daily cycle in the gravimetric water content at 5 cm indicates that moisture is absorbed by the soil during the late afternoon and night, and evaporating from morning to midday (Agam and Berliner 2004; Agam and Berliner 2006). The diurnal cycle of latent-heat flux is important and, in this study, observed through wet and dry seasons, hence it occurs independently of rainfall. Conversely, most meteorological models assume that in arid environments, latent-heat flux occurs only as a result of precipitation, and thus there is no latent-heat flux during the dry season (Agam and Berliner 2006). However, it has been recently found that the latent-heat flux involved in water vapour adsorption can reach higher than 20% of the net radiation flux (Agam and Berliner 2004; Katata et al. 2007), or total energy absorbed by the soil surface from all incoming and outgoing radiation. Latent-heat flux in this study caused an increase in soil moisture of between 10% and 25% during dry conditions (Fig 5.7), which is considerable when rainfall is absent over extended periods. The degree of latent-heat flux in arid ecosystems is often large and the assumption that no latent-heat flux occurs during dry conditions must be revised. Further studies are required to assess the contribution of atmospheric water vapour to soil moisture in arid zones, and its importance to sustaining arid communities and maintaining the soil-water balances during dry seasons.

During rain-free periods, soil moisture content was lowest between 6:00 am – 8:00 am, and highest between 1:00 pm – 3:00 pm. Peak evaporation at the study site occurs between 1:00 pm – 3:00 pm, and lowest evaporation occurs between 1:00 am – 5:00 am (Environdata 2019), hence soil moisture increases at 5 cm as evaporation draws moisture from lower depths to surface layers from morning until peak evaporation times, then decreases from late afternoon to dawn due to adsorption of soils (Katata et al. 2007). This information can inform land managers about when to schedule water and nutrient applications where applicable, but also has important implications for microbial communities as they are highly responsive to diurnal moisture and temperature fluctuations (Wang et al. 2013). For example, microbial activity of many Actinobacteria groups reduce from morning to night, whereas many Proteobacterial groups display the opposite trend (Gunnigle et al. 2017). Some studies suggest that non-rainfall moisture inputs are more important than rainfall or temperature in sustaining diverse microbial communities (Feng et al. 2014a; McHugh et al. 2015), and further studies are required to assess the importance of atmospheric moisture in driving microbial communities and soil moisture dynamics in arid zones.

5.5.3 Disturbance reduces moisture infiltration and retention

Reconstructing soils after mining reduces the water holding and infiltration capacities of soils, as predicted. Differences in soil moisture responses to rainfall generally increased with rainfall magnitude and, at 15 cm, soil moisture was always considerably lower at restoration zones. The largest rainfall event observed here (in December 2017) caused only marginal and short increases in soil moisture at 15 cm in rehabilitation sites (Fig 5.6). This suggests that reconstructed soils have increased evaporative water loss and/or run-off from the soil surface, which is likely caused by increased bulk density, compaction, electrical conductivity and pH observed at overburden rehabilitation sites at 15 cm depths (chapter four). The temporal period that rainfall remains at soil surface layers in arid zones is critical for plant survival (Allen et al. 2010), because evaporation rates are higher than rainfall across all months, and at least 10 fold greater than rainfall during summer months (chapter three). Soil texture and temperature, along with rainfall magnitude and time, determine the likelihood of evaporative moisture loss (Wythers et al. 1999). Changes to soil physical properties during disturbance and restoration have altered the water holding capacities and infiltration rates of soils and will likely exacerbate symptoms of water-stress for species on reconstructed soils when rainfall is persistently low.

5.5.4 Implications for restoration

Restoration areas showed lower rainfall infiltration than the remnant systems, and highlights a major challenge for the reconstructing of arid ecosystems. As demonstrated in chapter 4, the hydrological dynamics of soils at this study site have not been successfully reinstated by soil reconstruction, and this is likely to have major implications for the growth and persistence of vegetation on the site. Increased evaporation and/or run-off from surfaces of reconstructed soils is likely due to increased bulk density and compaction at depths between 5 cm - 15 cm (chapter four). Soil moisture infiltration and retention can be enhanced with irrigation, organic additives (Kidron and Tal 2012), and land contouring to promote water catchments (Bainbridge 2007; Bowker 2007). This study was conducted during a persistent drought, hence I could not assess important assumptions about soil moisture dynamics under large rainfall events as they didn’t eventuate. Further studies are recommended to determine water loss due to deep drainage, and the rainfall amounts required to stimulate plant-water use and productivity in arid tree species.

Arid ecosystems cover over 40% of the global land surface and are expected to expand under climate change (Reynolds et al. 2007). Climate models predict increasing fluctuations in temperature and timing of precipitation events across the globe (Meehl et al. 2000), with an overall increase in temperatures and greater unpredictability of rainfall in arid zones (IPCC 2012). Soil moisture responses from rainfall events are important drivers of plant productivity in arid zones, hence quantitative insights about important ecohydrological processes, such as this study, will enable more informed approaches to management (Abella 2012). Real-time soil moisture data from this study can also be used in conjunction with plant productivity and photosynthesis data acquired from remote sensing technologies, to accurately assess the amount of rainfall considered biologically significant for plants and microbes.

Soil moisture is a key criteria to restoring ecological function and ecosystem resilience to drought, hence methods to recreate soils that are resistant to evaporative water loss should be considered in all future arid restoration projects.

CHAPTER 6

Synthesis and implications for management

6.1 SUMMARY OF PROJECT AND RESULTS

One of the aims of the research presented in this thesis was to identify reasons for low rates of recruitment success in an arid ecosystem with reconstructed soils following mineral sand mining. It is important to understand recruitment dynamics and ecological function in natural ecosystems if we are to predict vegetation responses to land-use change and restoration methods. Seed survival and germination are linked to soil structure and moisture availability, hence this thesis investigates both of these elements. This synthesis of my results demonstrates some of the limitations to successful restoration in arid ecosystems, such as (1) unknown dormancy cues and poor seed longevity, (2) infrequent and episodic plant recruitment due to water limitation, and (3) reduced hydrological function of reconstructed soils. Results from this study suggest that restoration is possible and, in this chapter, I will synthesise my findings and suggest methods to improve restoration. I outline how my work contributes to the broader understanding of regeneration dynamics in arid ecosystems, address the implications for restoration at the local scale, and highlight knowledge gaps that should be addressed by future research.

6.2 BROADER IMPLICATIONS OF THIS STUDY

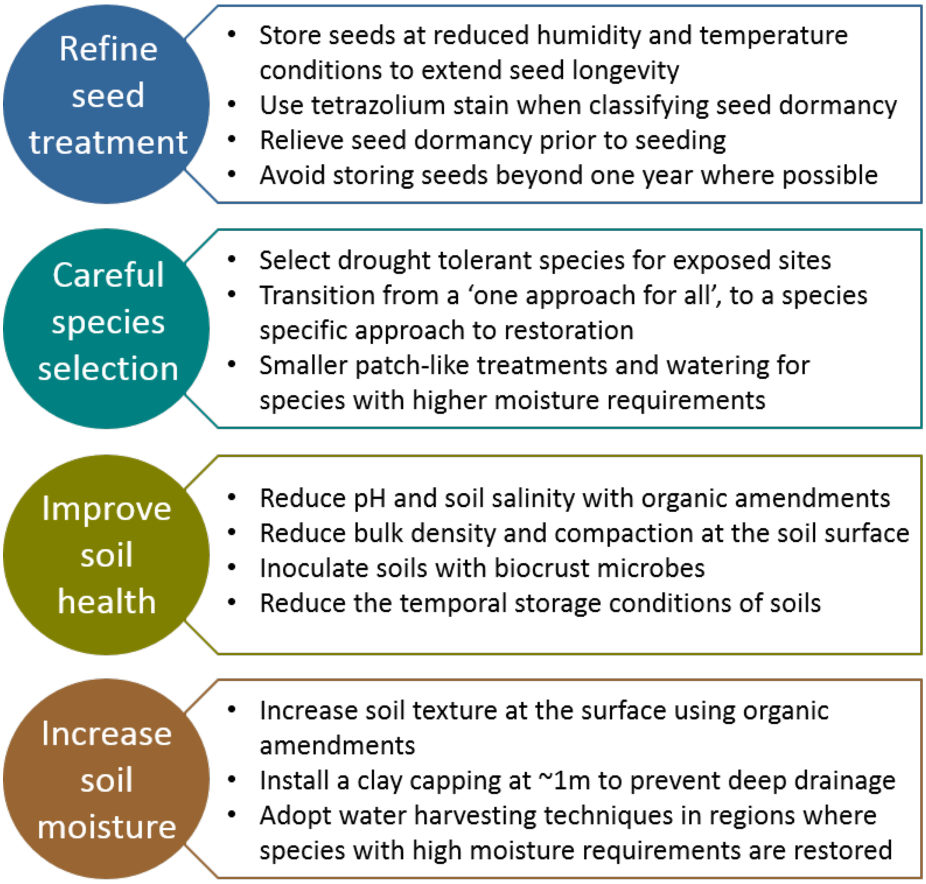
In arid regions, rainfall and soil moisture dynamics are the most important factors governing plant productivity and recruitment success (Chesson et al. 2004; Schwinning and Sala 2004). Indeed, this thesis demonstrates the importance of interactions among water, soil and seeds in arid landscapes. Certainly, arid species have evolved traits that allow them to persist and regenerate in dry conditions, and understanding these traits could provide insights that may aid their successful restoration. However, as this study shows, not all arid ecosystems are the same, and neither are species' responses to aridity. This study site is unusual because it does not have a reliable wet season, and this is the first study to demonstrate how unpredictable rainfall may affect the regeneration traits of arid vegetation. My results show that rapid germination is a common strategy in seeds from arid zone species, which allows seeds to capitalise on sporadic rainfall. Some species exhibited dormancy or bet-hedging strategies, which enables germination to coincide with periods of highest water availability. Similarly, high water potentials for germination was another important drought-avoidance strategy for arid species in this study.

Soil structure mediates the biological outcomes of rainfall events by determining the duration and volume of water that is available, hence disturbances to the soil profile in arid zones have consequences for the entire ecosystem (Macdonald et al. 2015; Sheoran et al. 2010). This study is the first to test these theoretical ideas in an arid ecosystem with unpredictable rainfall and I suggest that soil properties are the most crucial factor to control hydrological function in arid zones that experience regular droughts. Reconstructed soils in this study had high sand content at subsoil horizons and unfavourably high bulk density and compaction at surface layers (chapter four), whereas soils at remnant sites had course-textured topsoils that overlay clay subsoils. The specific arrangement of particle-size distribution observed at remnant sites are important for preventing water loss and maintaining hydrological function and plant productivity in arid zones (Noy-Meir 1973; Reynolds et al. 2004). This study shows that the organisation of the soil profile and the soil–moisture dynamics of remnant ecosystems are better suited to water retention than in the reconstructed ecosystem. Hence, the rehabilitated areas may have less ability to cope with extended drought and climate change than the remnant systems. Understanding the role soils play in mediating the impact of drought is increasingly important under climate change, considering the current expansion of arid zones globally (Cai et al. 2012; Huang et al. 2016a). Further studies that assess ecohydrological function, within the context of the biophysical constraints of native species, are crucial for conserving biodiversity and resources for humanity.

6.3 IMPLICATIONS FOR RESTORATION OF ARID ECOSYSTEMS

Restoration of arid ecosystems is particularly challenging because regeneration and growth of arid vegetation is closely tied to resource pulses that are typically rare in these environments. Reproducing these conditions and reinstating ecosystem function of a completely deconstructed ecosystem is a mammoth undertaking. Here, I will demonstrate how my research findings could help to improve the effectiveness of restoration methods in arid ecosystems generally, and in my study region specifically.

There are many factors to consider when restoring an arid ecosystem, which begins with reconstructing the physical environment; the soil structure. The post-mining sites in this study had lower rainfall infiltration and moisture retention than the surrounding remnant ecosystems, hence plants in these sites are subjected to altered moisture availability. While plant species in the arid zone have traits that help them cope with low soil moisture availability, the soil environment is structured in a way that allows plants to make the most of low rainfall. However, when the soil environment is removed, plants may be pushed beyond their limits despite traits that help them cope with low soil moisture. To overcome the consequences of soil reconstruction and poor restoration outcomes, I propose the following framework for restoration at the study site (Fig 6.1), and expand upon this framework in the following sections.



Refine seed treatment

- Store seeds at reduced humidity and temperature conditions to extend seed longevity
- Use tetrazolium stain when classifying seed dormancy
- Relieve seed dormancy prior to seeding
- Avoid storing seeds beyond one year where possible

Careful species selection

- Select drought tolerant species for exposed sites
- Transition from a ‘one approach for all’, to a species specific approach to restoration
- Smaller patch-like treatments and watering for species with higher moisture requirements

Improve soil health

- Reduce pH and soil salinity with organic amendments
- Reduce bulk density and compaction at the soil surface
- Inoculate soils with biocrust microbes
- Reduce the temporal storage conditions of soils

Increase soil moisture

- Increase soil texture at the surface using organic amendments
- Install a clay capping at ~1m to prevent deep drainage
- Adopt water harvesting techniques in regions where species with high moisture requirements are restored

Fig 6.1: Framework highlighting the key results from this study and methods to improve restoration outcomes at the study site.

6.3.1 Refine seed pre-treatment methods

Large-scale restoration projects, including this study site, usually involve a once-off, or yearly, application of seed (Corbett 1999), which rarely coincides with seed production. Therefore, seed storage is often unavoidable. This study was conducted during the most persistent drought in modern history and, in response to drought, many species did not produce a reliable seed supply. I studied the seed traits and germination strategy of keystone plant species to determine their regeneration strategies and found seed viability and longevity to be critical problem for some species. In particular, *M. platycarpum* survives < 3 months in storage, hence restoration from seeding efforts will rely on further studies aimed at extending seed longevity through reduced temperature and humidity treatments. Seeds used for restoration are currently stored on site in shipping containers, with temperatures maintained at 20-25°C, until restoration commences, which is typically many months, or even years, for some species. However humidity conditions in these shipping containers can often exceed 60% (Tim Zwiersen, personal communication, 21 February 2019) and, when humidity exceeds 40%, significant declines in seed longevity can be expected for many species (Pakeman et al. 2012; Suma et al. 2013). Improving seed storage conditions should be considered a priority at this study site. For most species in this study, viability declines drastically when seeds are stored beyond one year (Chapter 2), hence seed collection should be conducted on a yearly basis where possible. Storing seeds at cooler temperatures (~4°C) and reduced humidity may extend seed longevity, assuming seeds are non-dormant or temperature is not a factor controlling relief of dormancy. Regular seed collection can be problematic at the study site during drought conditions, further reinforcing the urgency for future studies aimed at extending seed longevity.

Two of the eight species in this study had physiological dormancy traits—*A. rhagodioides* and *G. parviflora.* As this study shows, dormancy should be alleviated in all species prior to seeding, to increase germination speed, provide wider temporal ranges for germination, and to reduce the chance of infection and death (Finch-Savage and Leubner-Metzger 2006). Restoration of species with elusive dormancy cues, including *G. parviflora*, may rely on tubestock technologies. When classifying dormancy, I caution against using visual assessments of embryo firmness and colour to determine seed viability, because it can lead to incorrectly classifying dead embryos as being dormant. At least 90% of seeds at the study site fail to pass the seedling emergence stage (chapter 1), which is representative of seed mortality rates for arid restoration projects globally, and a better understanding the dormancy cues and germination niche of species is crucial for reducing seed wastage (Merritt and Dixon 2011; Rokich and Dixon 2007; Wijdeven and Kuzee 2000).

6.3.2 Selecting suitable species for the restoration landscape

Plants exhibit a diverse set of traits enabling them to persist and reproduce in arid climates and such survival traits (including seed dormancy and drought avoidance) are not always conducive for their re-establishment under current management approaches. Water availability controls plant recruitment and productivity in arid zones, hence I investigated the role of water availability in the germination strategies of keystone species. Species adhered to either of two germination strategies: (1) the risk-takers with lower moisture thresholds for germination, and with wide thermal ranges for germination that are not narrowed at low water availability (*Casuarina pauper* and *Maireana pyramidata*), and (2) the risk-avoiders that have greater moisture requirements, a preference for cold climate germination, and narrower temperature ranges for germination when water availability is low (*Atriplex rhagodioides*, *Maireana sedifolia* and *Hakea leucoptera*). I suggest that species with high moisture requirements for germination are not suitable for broadcast seeding on exposed surfaces, particularly during drought conditions. Instead, drought tolerant species with lower moisture requirements and rapid germination, such as *M. pyramidata*, will likely perform better in these restoration landscapes. This is supported by current restoration outcomes, because *M. pyramidata* typically dominates the restoration landscape (see Chapter 1). As *C. pauper* was the only tree species to germinate within a few days, I suggest it to be a potential candidate for regeneration from broadcast seeding efforts, assuming high moisture is retained in soils for at least a few days.

For tree species that require higher moisture availability for longer to germinate, I recommend changing restoration methods from a ‘one approach for all’, to a ‘species-specific approach’. If slow-to-germinate species, such as *A. oleifolius* at winter temperatures, and tree species with high moisture requirements for germination (including *Hakea* species), are to be restored via seeding then they may require additional assistance, such as engineering rehabilitation zones to increase temporal water availability. Most species in this study are adapted to avoid germination in drought conditions, therefore techniques to enhance water availability may be crucial to reinstate these woody species. However, whether species survive moderate or severe droughts in the restoration landscape warrants further investigation. The reconstructed soils I studied are less resistant to water loss, hence may not be suitable for species that avoid or delay germination under dry and hot conditions (*A. rhagodioides* and *M. sedifolia*, and particularly for *H. leucoptera).* Nonetheless, re-establishing such species on reconstructed soils may be possible if they are managed as water-stress sensitive species with episodic recruitment, and that means engineering soils to increase available water, and seeding when temperatures are cooler and the temporal window for moisture retention is wider (i.e., during mid-winter; Chapters 2 and 3).

6.3.3 Improving soil health

The organisation of soil layers, according to particle size, has important implications for restoration success. Soils in unmined remnant sites have characteristics that resist water loss: high sand content in the upper soil layers to enhance infiltration, and high clay content at lower depths to prevent water leeching beyond maximum root zone depths (Chapter 4). Conversely, mined sites had courser soils at depths below 85 cm and unfavourably high bulk density and compaction at surface layers (0 – 20 cm). Thus, mining practices and subsequent restoration attempts have resulted in significantly altered soil structure and properties that are important for plant growth, particularly variables associated to the distribution of particle-size content and salts. Low clay content below the root zone is potentially disastrous for restoring species in this arid zone because plants rely on large rainfall events to grow and recruit, and moisture from large rainfall events may potentially be lost to deep drainage. Furthermore, high bulk density and compaction at upper soil surface layers facilitate higher evaporative water loss and run-off from small rainfall events, essentially reducing the amount and time that water is available for plant uptake. Increased bulk density in topsoil restricts the root growth and productivity of plants (Singh et al. 2015) and high compaction at near-surface layers drastically reduces soil resistance to moisture loss. Minimising heavy tractor use to reduce surface compaction and bulk-density must be considered in future restoration efforts to reduce compaction of topsoils, and subsequently to reduce evaporative water loss and improve soil quality and plant health.

Reconstructing soils at this study site also reduces microbial activity, and increases soil pH and variables associated with salts (Chapter 4). These soil properties further impact water availability and plant-water uptake, and are key barriers to restoration in this arid zone. Microbial activity decreased with time since restoration. The exception to this trend was the oldest mined site, which had the highest microbial activity, but was excluded from analysis as it was the only site with microbial inoculates added to soils during reconstruction. This result may indicate that there are long-term benefits to treating topsoils with microbial inoculates. To ameliorate low microbial activity and increased soil pH and salinity, I recommend treating topsoil with amendments of coarsely-ground organic matter (Sheoran et al. 2010), and taking greater care to prevent the mixing of subsoils with topsoils during soil removal and replacement. Storage of topsoils for extended periods can deplete soil health (Carrick and Krüger 2007; Graham and Haynes 2004; Kundu and Ghose 1997), hence I encourage the mine site to persist with the practice of immediately reapplying topsoils to restoration sites whenever possible (a process known as direct return; Grant et al. 2016).

6.3.4 Increasing soil moisture

Chapter 5 is the first study (to my knowledge) to quantify the fate of water from rainfall events, in real-time, in an arid ecosystem in remnant and reconstructed states. Our understanding of the temporal link between rainfall, soil moisture and ecological feedbacks remains largely theoretical, but my results revealed some important aspects of soil moisture dynamics in the reconstructed soils. I installed soil moisture monitoring probes, with five sensors at depths to 90 cm, in arid woodland and shrubland sites, and in reconstructed soils, and monitored soil moisture hourly for over one year. Small rainfall events (< 10 mm) were most common, but did not affect soil moisture at depths below 5 cm. Large rainfall events > 20 mm were not recorded during this study, and no changes to soil moisture at depths below 15 cm were recorded in response to any rainfall event. As such, the rainfall required to increase soil moisture below 15 cm depth is unknown. Soil moisture infiltration and retention at 15 cm was less in the reconstructed soils than in the remnant ecosystem, likely caused by less infiltration, increased run-off and/or increased evaporation. This is probably caused by increased compaction and bulk density at this depth in reconstructed soils, as recorded in chapter four.

Soil moisture responses from rainfall events are important drivers of plant productivity in arid zones and I suggest that increased bulk density and compaction at depths between 5 cm - 15 cm impedes ecohydrological function in reconstructed soils. As mentioned above, increased compaction and fine particle content at lower depths are crucial to prevent water leeching to depths lower than roots of arid plants (Sala et al. 1988). However, my data showed that reconstructed soils had low fine particle content at depths below 85 cm. This study was conducted during a persistent drought, hence I could not assess important assumptions about soil moisture dynamics under large rainfall events as they didn’t eventuate. Further studies should determine water loss due to deep drainage. I suggest that the failure to recreate ecohydrological function is the key barrier to restoration in this arid ecosystem. Methods to increase the temporal and spatial availability of soil moisture should be considered as a priority for improving restoration outcomes in this arid zone. I recommend integrating *in-situ* water-harvesting techniques in management plans to improve soil health, moisture retention and subsequent restoration outcomes. Methods to reduce evaporative water loss from soils may include restoring biocrusts (Bowker 2007; Kidron and Tal 2012), planting cover crops, irrigation, organic additives and land contouring to promote water catchments (Bainbridge 2007). Water-harvesting techniques become more important in the restoration of species with high moisture requirements for recruitment and productivity. Chenopods recruited poorly across the rehabilitation areas during this study, due to drought conditions, but recruited well at one site with unintentional surface drainage (Fig 6.2). This suggests that water-harvesting techniques will be beneficial for plant recruitment in this arid zone. Soil moisture is a key criteria to restoring ecological function and ecosystem resilience to drought, hence methods to enhance water availability should be considered in all future arid restoration projects.

Fig 6.2: Restoration at the Ginkgo mine site in 2018 shows successful recruitment during recent years of drought conditions. Although plant establishment has since been affected by the current drought, the photo (taken by Tim Zwiersen, 2018) demonstrates how unintentional surface drainage has resulted in the establishment of a chenopod species in spite of poor seasons.

6.4 FURTHER RESEARCH

Reinstating hydrological processes is a key challenge for mine site restoration in arid zones. Technical knowledge about recreating soils that are resistant to water loss is urgent, and will involve concepts of inducing water run-off and enhancing water storage. Organic amendments may enhance soil moisture storage, although prior to introducing large quantities of foreign organic fractions to impoverished soils, further field experiments should be conducted to understand decomposition rates of soils with organic amendments, plant responses to increased nutrients, and to identify microbial taxa present in soils and their physiological responses to changes in soil condition. Soil reconstruction in this arid ecosystem disorganises the arrangement of particles that promote resistance to water loss. To reinstate important hydrological cycles, further research is required into alternative soil-replacement techniques to increase sand content at surface layers, and decrease sand content at maximum root zone depths. Further studies into water loss due to deep drainage and plant-water use from large rainfall events are also critical. Identifying the key causes of moisture loss in reconstructed soils and ameliorating hydrological function will require new experimental and quantitative insights, and should be the central focus of all large-scale restoration projects in arid regions. My data showed that the rehabilitation sites experienced less rainfall infiltration from rainfall events, and that increases in soil moisture did not last as long as in the remnant ecosystems. As such, the remnant ecosystems could provide insights into how arid ecosystems will function if long-term average rainfall decreases and rainfall variability increases.

Arid plants exhibit traits to prevent emergence and growth during dry conditions and, as this study has shown, most species avoid germination during drought. Questions remain surrounding alternative and sustainable intervention methods to support the recruitment of drought-avoiding or water-stress sensitive species. The ‘one method for all species’ approach to restoration—i.e. broadcast seeding and deep ripping soil—is not effective for water-stress sensitive species, nor for woody species that require water for longer to regenerate. Alternative approaches to restoration that more accurately mimic natural processes are necessary to overcome high recruitment failures and re-establish the full suite of species observed prior to disturbance. Such new and innovative restoration methods should be trialled at restoration sites, and these trials should include sound experimental design and rigorous monitoring so that the outcomes can be objectively evaluated, and our collective knowledge of arid restoration techniques can be improved.

My study did not investigate the spatial organisation of resources above the soil surface in these arid ecosystems, but this is another aspect of arid ecosystems that can serve to enhance soil moisture retention. The concept of run-off and run-on zones (Ludwig and Tongway 1995) describe how soil moisture can be heterogeneously distributed within a system, and how vegetated ‘run-on’ zones can have higher effective soil moisture than the climate and annual rainfall would otherwise suggest. Research is needed into how to recreate patch dynamics and islands of fertility (Bolling and Walker 2002; Ridolfi et al. 2008), to increase soil moisture and improve restoration outcomes. Innovation may be required to successfully apply these concepts across large spatial scales in a restoration setting, but the pay-off could be significant. To date, restoration at these mines has attempted to recreate a homogenous landscapes, hence it is difficult to determine if the lack of heterogeneity in the organisation of above-ground resources has limited restoration success. I suggest this is an important area for future research.

This thesis has contributed to our understanding of the factors limiting seed germination, but the post-germination success of different species in this highly disturbed and highly stressful environment requires further investigation. Indeed, an understanding of the environmental and biological filters that might limit seedling survival and growth could greatly improve restoration success. Early successional (ruderal) plants often recruit more readily in disturbed environments (Grime et al. 1981) and can modify soil properties and microclimatic conditions to facilitate the recruitment of later successional plants (Connell and Slatyer 1977). The stress gradient hypothesis predicts that facilitation prevails in stressful environments (Bertness and Callaway 1994; Maestre et al. 2009), and understanding these positive plant-plant interactions could be pivotal for arid ecosystem reconstruction (Gómez-Aparicio 2009). To date, restoration has been attempted with all target species in the initial seeding mix, but a staged approach to introducing species might achieve greater success, and more efficient use of seed.

Soil degradation is a key threatening process in arid ecosystems under land-use and climate change (Plaza et al. 2018) and current global approaches to large-scale restoration projects are insufficient when applied to arid zones. Nonetheless, restoration is possible with further research and more informed management decisions. Novel ecosystems require novel management approaches and our poor track record of restoring arid ecosystems does not imply that ‘all bets are off’, but instead highlights the need for rapid knowledge transfer and research–driven management activities (Seastedt et al. 2008). Fortunately, nature provides the perfect learning platform to recreate, or mirror, important biological and ecological processes.

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