Cracking the Niche:

An investigation into the impact of climatic variables on germination of the rare shrub *Verticordia staminosa* subspecies *staminosa* (Myrtaceae).

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Impact of climatic factors on germination of the rare shrub *V. staminosa*

**Declaration**

This thesis is my original work and has not been submitted, in whole or in part, for a degree at this or any other university. Nor does it contain, to the best of my knowledge and belief, any material published or written by another person, except as acknowledged in the text.

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Gregory Douglas Simpson

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**Abstract**

The influence of annual rainfall and a Mediterranean climate in structuring the indigenous vegetation in the Southwest Botanical Province of Western Australia has long been recognised, especially in relation to seedling germination during the cooler wet season. However, over the past decade numerous authors have hypothesised that a number of climatic factors, including variability in the timing and intensity of rainfall events, may be drivers of germination. *Verticordia staminosa* subsp. *staminosa* (Myrtaceae) is a naturally rare narrow range endemic shrub that occurs on only one granite inselberg near Wongan Hills in the ‘wheatbelt’ of southwest Western Australia. Smoke and fruit wall weathering have been claimed to be specific dormancy breakers for the seeds of many Australian genera, including *Verticordia*. However, I found no evidence of smoke and artificial weathering influencing germination of *Verticordia staminosa*. Using data from a long-term (12 year) investigation into field germination of *Verticordia staminosa*, my thesis applies logistical regression techniques to model the impact of climatic variables on germination within the only recorded *Verticordia staminosa* subsp. *staminosa* meta-population. My analyses reveal that a complex interplay of the amount of rainfall, number of rainy days, diurnal temperature range, and storms related to tropical cyclones/lows, under a traditional four seasons or six Noongar seasons climate, best describes the observed germination of *Verticordia staminosa* seedlings.
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Chapter 1: Introduction and Thesis Organisation

1.1 Introduction

At the start of the 20th century Fredrick Clements (1905) wrote “the factors of a habitat are water-content, humidity, light, temperatures, soil, wind, precipitation, pressure, altitude, exposure, slope, surface (cover), and animals”. A foundation researcher in the field of Ecology, he went on to say that “length of season” was an important and complex influence on vegetation that should “be treated under its constituents”, that is humidity, light, temperature, wind, and precipitation. While Clements provided this sage advice over 100 years ago, little progress has been made in elucidating the impact of climate variables on recruitment, even for the highly studied vegetation found in Mediterranean climates. In a review of how plant life-history and ecological traits relate to rarity or commonness, Murray et al. (2002) found that “a large proportion of studies” are based on small sample sizes with little replication and that duplicate studies “overwhelmingly … differ from one and other in their findings”. When writing about the impact of climate change on Australian ecosystems and native species Hughes (2003) said:

“Predicting what will happen to species distributions in the future must rely heavily on understanding the [climatic] factors by which they are currently limited. Although the question ‘What determines the distribution and abundance of species?’ is fundamental in ecology, we do not know the answer to it for any more than a handful of Australian taxa.”

Cody (1986) and Cowling et al. (2005) both identify the need to more fully investigate the impact of environmental variables on germination in Mediterranean climates, specifically in terms of rainfall variability in the southwest of Western Australia. More recently, Yates and Ladd (2010) concluded that in relation to vegetation in the fragmented landscape of south-western Australia the “effects of climate change on the persistence of rare species … are now being recognised as an area in need of investigation”. The predicted increase in temperatures and decrease in precipitation over most of Australia over the second half of this century further increases the importance of characterising climatic thresholds for vegetation (Christensen et al. 2007; Fischlin et al. 2007; Hughes 2003; Cochrane and Daws 2008).

Characterising every abiotic and biotic factor that impacts seedlings germination for the naturally rare shrub Verticordia staminosa subsp. staminosa (Gardiner
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and George 1963) to define its realised regeneration niche is clearly beyond the scope of an Honours project. Following MacArthur’s (1968, cited in Krebs 1994) recommendation to describe a niche in terms of a limited number of quantifiable variables, my research investigates possible relationships between climatic variables, fruit being exposed to smoke and weathering, and the quantity and rate of *Verticordia staminosa* subsp. *staminosa* seedling emergence. To illuminate any relationship between these parameters I constructed a number of metrics to explore differing hypothesis by applying multivariate statistical techniques to the analysis of both long term (12 years) germination data maintained by the Department of Environment and Conservation and for data I generated in glasshouse germination trials. Specifically I propose the null hypotheses that germination of *Verticordia staminosa* subsp. *staminosa* is not impacted by:

- The amount and/or timing of rainfall.
- Air temperature.
- Non-climate variables, such as the age of fruit (hereafter pericarp), the exposure of the pericarp to smoke, and/or weathering of the pericarp.

The experimental design and statistical analyses I apply in this study allowed me to investigate the appropriateness of both Eurocentric and Noongar seasons to elucidate the impact of climatic variables on the germination of *Verticordia staminosa* subsp. *staminosa* (hereafter *V. staminosa*, unless otherwise specified).

### 1.2 Organisation of this Thesis

This thesis is structured so that each chapter provides information and builds an understanding of the material that is presented in the following chapter. The structure of my thesis and a brief overview of each chapter appear below.

**Chapter 1: Introduction.** This chapter provides a rationale for my investigations, defines the research questions that I explore in the study (null hypotheses), outlines how my thesis is structured, and how my understanding of the variables that influence *V. staminosa* germination developed.

**Chapter 2: Literature Review.** This chapter provides background to the major topics of my thesis: the biogeographical characteristics of the Southwest Botanical Province (particularly in relation to *V. staminosa*), the importance of the regeneration niche for persistence of *V. staminosa*, which climate variables (e.g. amount of rainfall, maximum and minimum temperatures) impact the life...
histories of vegetation, and the character of the climate and structure of the seasons in southwest Western Australia.

**Chapter 3: Methods.** I start this chapter with an overview of the field study site and the species *V. staminosa*. Next I outline my experimental approach to gathering the data for my research before moving on to detail my approach to statistically analysing that data.

**Chapter 4: Results.** Detailing the findings of my project, this chapter progresses from the insights I gained in the exploratory data analyses and through my investigation of the soil seed bank. It provides evidence of the three different patterns of season in southwest Western Australia, and concludes by presenting and ranking a series of logistical models that describe how climatic variables impact *V. staminosa* germination.

**Chapter 5: Discussion.** I use this chapter to describe the understandings that I developed during this study and to place the outcomes of my research in context with the findings and hypotheses reported in the published works of other researchers.

**Chapter 6: Conclusion and Recommendations.** I conclude my thesis by providing a summary of the most significant findings from my research. I revise the research questions specified in the Introduction of my thesis, pose alternate hypotheses informed by my research, and make recommendations for additional research that will build on this study and further illuminate the variables that most significantly impact germination of the indigenous vegetation of the Southwest Botanical Province.


Chapter 2: Literature Review

2.1 Southwest Botanical Province of Western Australia

Located in the south western corner of the Australian continent and covering approximately 360,000 km², the Southwest Botanical Province of Western Australia (SWBP) is bound by the Indian Ocean, the Southern Ocean, and a diagonal line running southeast from the southern end of Shark Bay to approximately Esperance (Israelite Bay) in the south (Beard 1980; Gole 2006). The SWBP is analogous with both the slightly smaller (300,000 km²) Southwest Australian Floristic Region (SWAFR) of Hopper and Gioia (2004) and the Bibbulman Country that the Noongar people have occupied for the past 50,000 years (Gole 2006; South West Aboriginal Land and Sea Council 2011). Somewhat confusingly WWF-Australia groups the SWBP with the more arid "Transitional Zone" to the east, which is different to the "Transitional Rainfall Province" proposed by Hopper and Gioia (2004), to create the slightly larger (490,000 km²) Southwest Australia Ecoregion (Gole 2006).

With a climate of warm dry summers and cooler wetter winters, the SWBP is one of the five Mediterranean climate regions spread around the planet, the other four are centred on northern Africa/southern Europe (Mediterranean basin); California; Chile; and the Cape region of southern Africa (Cody 1986; Lamont 2004; Cowling et al. 2005). Covering less than 5% of the Earth’s surface these five regions contain almost 20% of the known vascular plants species, many of which are rare narrow range endemics (Cowling et al. 1996; Hopper and Gioia 2004).

The combination of bimodal (dry season/wet season) climate, frequent fires due to summer aridity (expect for Chile), and/or isolation of habitats over geological timescales by both natural land forming processes and fragmentation by humans (thorough activities such as agriculture, logging, and more frequent fire regimes) has resulted in these bioregions having exceptionally high alpha (α), beta (β), and gamma (γ) diversity compared to other temperate biomes (Attiwill and Wilson 2004; Hopper 1979; Cody 1986; Cowling et al. 1996; Lamont 2004). Among the most floristically diverse places on the planet, sites within the SWBP have species richness comparable to tropical rainforests and the fynbos vegetation of the southwest Greater Cape Floristic Region in Africa (Groves and Catling 2004; Cowling et al. 1996). A millennia of biological isolation after Australia rifted from Antarctica between the mid-Cretaceous (130 Million Years
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Before Present [MYBP]) and the Oligocene (45 MYBP), the mass loss of angiosperms during the K-T extinction event (66 MYBP), and increased aridity during the late Tertiary (11 MYBP) and mid Quaternary (0.025 to 0.015 MYBP) driving the differentiation and speciation has resulted in between 70% and 80% endemism (at least 3,500 species) for vascular flora of the SWBP (Attiwill and Wilson 2004; Hill and Brodribb 2004; Hopper and Gioia 2004; Raven et al. 2005). Further, many of the species, sub-species, and varieties of the SWBP are considered narrow range endemics and may occur as a single population or across a few disjunct meta-populations (Hopper et al. 1997; Hopper 2009; Withers 2000).

While one of the most species rich regions on the planet, since the introduction of European agricultural practices less than 200 years ago over 70% of the indigenous vegetation has been cleared from the SWBP (Myers et al. 2000). As a result at least 351 vascular plant species and the fauna they support are at risk of extinction, giving Australia’s southwest corner the shameful distinction of being labelled a Global Biodiversity Hotspot (Myers et al. 2000; Gole 2006).

**2.2 Defining the Regeneration Niche for *V. staminosa***

**2.2.1 Defining a Species’ Niche**

The 3rd edition of the Oxford Dictionary of Ecology notes that the range of a species is both “the entire geographical area over which it occurs” and “the spread of environmental conditions within which it occurs”. This broad meaning encompasses not only the current spatial distribution of a species, but also the abiotic and biotic aspects of its habitat and the temporal variability as ranges expand or contract across a season, a year, a decade, a century, a millennia or even geological time (Kruckeberg and Rabinowitz 1985; Dynesius and Jansson 2000; Attiwill and Wilson 2004).

At the time Clements (1905) was postulating which environmental variables constitute the habitat of a species, Grinnell (1904) wrote that it was not possible for two species (or subspecies) adapted to the same environmental “conditions” and/or “food habits” to exist without competing for resources and “only by adaptations to different sorts of food, or modes of food getting, that more than one species can occupy the same locality.” Developing this hypothesis further, he was among the first Ecologists to suggest segmenting a habitat into “niches” such that no two species occupying the same range could have “precisely the
same niche relationships” (Grinnell 1917). Many authors credit C.S. Elton’s 1927 book Animal Ecology (cited in Krebs 1994) with advancing Grinnell’s concept by defining a niche as a species’ role within its community. However, Udvardy (1959) thought that Grinnell’s concept of niche was complementary with Elton’s hypothesis that “the 'niche' of an animal means its place within the biotic environment” (quoted in Udvardy 1959 and Krebs 1994). Building on the work of Grinnell and Elton, as expanded by Lotka, Volterra, and Gause (Udvardy 1959; Krebs 1994), Hutchinson (1957) defined the “fundamental niche” of a species to be an "n-dimensional hypervolume \([N_1]..., every point in which corresponds to a state of the environment which would permit the species \(S_1\) to exist indefinitely.” Hutchinson proposed that for a second species (\(S_2\)) there would a corresponding hypervolume \((N_2)\) and as no two species can occupy exactly the same niche he went on to define “the realised niche \(N'_1\) of \(S_1\) in the presence of \(S_2\) as \((N_1 - N_2)\), if it exists, plus that part of \(N_1 \cdot N_2\) as implies survival of \(S_1\), and similarly the realised niche \(N'_2\) of \(S_2\) as \((N_2 - N_1)\), if it exists, plus that part of \(N_1 \cdot N_2\) corresponding to survival of \(S_2\) [bolding Hutchinson’s emphasis, italics are mine].”

2.2.2 The Regeneration Niche

The above theories arose from studies of competition among animals, primary in relation to food and physical resources (e.g. nesting and roosting sites) within their habitat. Grubb (1977) proposed that for plants the fundamental and realised niches should be further subdivided with the habitat niche, time niche, growth form niche, and regeneration tactics niche being key for defining which species can coexist. Mature plants can generally cope with a relatively wide range of environmental conditions, but species often require very specific conditions for regeneration (New 2004; Cowling et al. 2005; Fenner and Thompson 2005; Merritt et al. 2007). Grubb (1977) wrote that of the four niche types listed above, the “regeneration tactics niche” was the most important. He postulated this is because the death of any plant creates a space in the regeneration niche and whether that space is filled by an individual of the same species or colonised by an entirely different species depends on:

a) Plant processes in terms of reproductive capacity (by seed or vegetatively), dispersal, germination, establishment, and onward growth; and

b) Characteristics of the space such as size, shape, method and timing of its creation, disturbance of the growing medium (soil and litter), climatic conditions, plant/animal species present, and so on.
It should be noted that while the concept of the niche is generally accepted as a foundation theory of Ecology, not all researchers support this view and a study by Richardson et al. (1995) found lower diversity than that predicted by niche differentiation and no conclusive evidence of a regeneration niche.

### 2.2.3 The Regeneration Niche for V. staminosa

A combination of climatic variables (predominately rainfall) and the density of crevices (with suitable micro-habitat) in the granite pavement of the inselberg on which *V. staminosa* occur appear to be the primary determinants of abundance and distribution of the species (Yates and Ladd 2004; Yates et al. 2007). An increase in both germination and survival of *V. staminosa* seedlings has been observed in a year when the rainfall was substantially greater than the long term annual mean (Yates and Ladd 2004).

### 2.3 Seed Dormancy and Germination Stimuli

#### 2.3.1 Seed Dormancy

The term ‘seed’ is generally taken to mean the embryo plant and the protective seed coat, that is the testa and, where present, the hard outer capsule or pericarp (Leopold 1964). However, when discussing seed dormancy it is more appropriate to apply the definition of Fenner and Thompson (2005) that a seed is just the embryo plant excluding the seed coat.

Dormant dispersed seeds are prevented from responding to environmental germination stimuli by a single or more often a combination of morphological, physical, or physiological mechanisms (Leopold 1964; Fenner and Thompson 2005; Merritt et al. 2007). Overcoming morphological dormancy, which arises when fruit are dispersed before the seed has completely matured, requires additional development of the seed before germination can occur (Pickup et al. 2003; Fenner and Thompson 2005). The most common dormancy state or syndrome, physiological dormancy is alleviated by a change in the seed that overcomes inhibitor chemicals contained within the embryo or generated by the seed coat (Leopold 1964; Pickup et al. 2003; Fenner and Thompson 2005). Physical dormancy is imposed by the seed coat restricting space for the embryo to develop, being impermeable to respiration gases, and/or more commonly being impermeable to moisture (Leopold 1964; Fenner and Thompson 2005; Merritt et al. 2007). While light may play a role, temperature alone has been demonstrated to alleviate both physical and physiological dormancy by cracking
the seed coat or increasing its permeability and by facilitating chemical changes in an imbibed seed (Leopold 1964; Fenner and Thompson 2005; Merritt et al. 2007). While morphological and physical dormancy cannot be reimpied once alleviated; a seed that has been released from dormancy and imbibed, but not stimulated to germinate, may redry and enter (or return to) a state of secondary physiological dormancy (Fenner and Thompson 2005; Merritt et al. 2007).

A seed’s state of dormancy can only be assessed by observing if it develops when exposed to germination stimuli such as temperature, moisture, light, and/or chemicals, for example gibberellins, nitrates, or smoke (Pickup et al. 2003; Fenner and Thompson 2005). Determining if a seed is dormant or if it is imbibed but inactive can be a difficult and contentious assessment (Pickup et al. 2003; Fenner and Thompson 2005; Merritt et al. 2007; Cousens et al. 2010).

2.3.2 Germination Stimuli

Growth of a seedling is the outcome of the progression through the separate but closely coupled processes of the seed being released from dormancy, imbibition of the non-dormant seed, and the response of the imbibed embryo to germination stimuli (Pickup et al. 2003; Fenner and Thompson 2005; Merritt et al. 2007). As mentioned previously, temperature is the only environmental factor that has been demonstrated to alleviate dormancy and all other aspects of the seed’s microenvironment become germination stimuli (Fenner and Thompson 2005; Merritt et al. 2007). This is a marked shift from the historical view of dormancy-breaking by chemical (e.g. gibberellins and smoke), light and photoperiod, moisture (e.g. wetting/drying cycles), and/or temperature (e.g. stratification) treatments (Leopold 1964; Dixon et al. 1995; Hopper et al. 2006). This shift in understanding is illustrated by the change in language from the hypothesis of Dixon et al. (1995) that ammonia/ammonium in smoke “might be one of the agents active in breaking dormancy” to the observation in Merritt et al. (2007) that “the action of smoke as a germination stimulant, rather than a dormancy-breaking agent, is becoming clearer.”

2.3.3 Weathering and Seed Imbibition

Many studies of germination of Australian hard seeded species report the requirement for a period of ‘dry after-ripening’ (morphological dormancy) and enhanced rates of germination for soil stored seed as compared to fresh seed and laboratory stored seed banks (Pickup et al. 2003; Merritt et al. 2007; Martyn
et al. 2009; Cousens et al. 2010). Morphological dormancy in SWBP soil seed banks avoids fresh seed competing with primed seeds (i.e. dormancy alleviated and imbibed) and prevents late winter rain stimulating germination without sufficient ongoing soil moisture for the seedling to establish prior to the summer drought (Tieu and Egerton-Warbuton 2000; Pickup et al. 2003; Martyn et al. 2009; Cousens et al. 2010). As outlined in Section 2.3.1, the enhanced germination of soil stored seeds following a period of dry after-ripening is attributed to temperature and (possibly) moisture cues in alleviating physiological and physical dormancy (Pickup et al. 2003; Merritt et al. 2007; Cousens et al. 2010). Physiological dormancy is alleviated through natural stratification during periods of elevated soil temperatures and increased moisture from (generally) light early season rains from March to May (Baker et al. 2005; Fenner and Thompson 2005; Merritt et al. 2007). Physical Dormancy is alleviated through weathering (temperature and moisture cycling) weakening the seed coat to increase its permeability to water and gases or in the case of hard seed by cracking the pericarp (Tieu and Egerton-Warbuton 2000; Lush et al. 2003; Pickup et al. 2003; Merritt et al. 2007). Although Martyn et al. (2009) and Cousens et al. (2010) have recently challenged the premise that the pericarps of hard coated Australian seeds enforce physical dormancy through imperviousness to moisture that is alleviated by weathering. Both studies found that hard coated seeds rapidly absorb moisture and start to imbibe within 24 hours of being exposed to available soil moisture. Similar to the findings of Lush et al. (2003), these two papers hypothesise that the seed coat reduced desiccation of the seed during dry periods between rain events promoting an incremental or “stop-go” process of imbibition and germination. Despite differences in view about the moisture permeability of pericarps, all three studies found that fluctuations in temperature and moisture (wetting and drying cycles) experienced by a hard coated seed in the soil degrades and cracks the seed coat, alleviates primary and secondary physiological dormancy, and enhances imbibition of the seed increasing the rate of germination.

2.4 Modelling the Impact of Climatic Variables

The exceptionally high diversity, geographical isolation, and climatic similarity of the Mediterranean regions has generated many studies of convergent and divergent evolution (Cody 1986; Cowling et al. 1996; Lamont 2004). It would seem reasonable to assume that a number of these studies would have
investigated the impact of climate on regeneration. However, the majority of vegetation studies fail to consider the impact of climatic variables or any reported relationships are often based on only a cursory analysis (Cody 1986; Murray et al. 2002; Hughes 2003; Cowling et al. 2005). With increasing concern about the impact of rapid climate change on the range and survival of species, there is growing recognition of the need to predict changes in distribution and likelihood of climate induced extinction (Hughes 2003; Fay 2009; Tarroso and Rebelo 2010; Yates and Ladd 2010).

2.4.1 What ‘Climatic Variables’ to Model?

While Clements (1905) recognised the importance of humidity, light, temperature, wind, and precipitation in defining a plant’s habitat, what metrics and interactions of these environmental variables are significant for germination?

Annual rainfall has long been recognised as an important determinate of species distribution (Gardner 1959; Hooper 1979). Increasingly authors are also recommending that variations in the seasonality of rainfall, the frequency of rainfall events, and the amount of rainfall and duration (i.e. intensity) of individual events be considered (Cowling et al. 2005; Fay 2009; Robertson et al. 2009).

In addition to these precipitation predictors, Tarroso and Rebelo (2010) also identify the month to month variation in the monthly average temperature, monthly average maximum temperature, monthly average minimum temperature, diurnal temperature range, vapour pressure (i.e. evaporation and/or humidity), cloud cover, and (where appropriate) frequency of frost free days. At a finer spatial and temporal scale, Fontaine et al. (2010) assessed the daily (24 hour) maximum, minimum, diurnal range, and mean air temperatures (1m above soil surface); the mean daytime temperature (7am to 6pm); the mean ‘heating’ temperature (9am to 2pm); and the mean cooling temperature (4pm to 9pm) at multiple locations in logging stands post wildfire. This study identified the need to investigate additional climate related variables such as soil temperatures, relative humidity, and wind.

Another factor that warrants investigation is the potential for intense summer deluges, resulting from the passage of cyclones and topical storms, to influence _V. staminosa_ germination (White et al. 1999; Cowling et al. 2005).
Providing a practical example of how such modelling can be applied, Nicholls et al. (2001) were able to develop ‘skilful predictions’ of wheat yields using monthly rainfall values and diurnal temperature range as predictors.

2.4.2 What are the Seasons of South-West Western Australia?

The influence of annual precipitation in structuring the vegetation associations of the SWBP has long been reported by botanists, but the classic Mediterranean warm dry summers and cooler wetter winters is also known to be significant (Gardner 1959; Mott 1972; Brown 1989). What evidence is there about the seasonality of climatic metrics in south-west Western Australia?

The Mediterranean nature of weather in south-west Western Australia (hereafter SWWA) has been recognised from the earliest days of the Swan River Colony, however there has been less clarity about which months constitute the ‘warm dry summer’ and ‘cooler wetter winter’ (Curlewis 1929 and Wells 1884 quoted in Western Australia. Indian Ocean Climate Initiative (IOCI) Panel 2002; Nicholls et al. 1999; Cowling et al. 2005). Wells (1884) wrote “The wet season commences with light showers in April, which continue to increase in number and force throughout May, June, and July, and from that period decrease until they cease altogether, in the month of November, when the dry weather begins”. Based on evidence from rainfall, both Dirnböck et al. (2002) and Cowling et al. (2005) classified April to September as the southern hemisphere winter and consequently summer occurs from October to March. However, W.J. Wright (1997) found that 80% of the SWWA’s precipitation fell from May to October and the Australian Bureau of Meteorology Research Centre assigns these months as SWWA’s ‘winter’ period (Nicholls et al. 1999). Two major rainfall variability signals have been noted within the bimodal climate of SWWA. In most years more rain falls in early winter with August to October being dryer (Wells 1884; P.B. Wright 1971, cited in Allan and Haylock 1993; P.B. Wright 1974), and occasionally deep penetrating tropical cyclones transport moisture from northern latitudes into the SWWA causing large summer rainfall events (Milewski 1979, cited in Cowling et al. 2005).

Early European settlers also applied the traditional ‘Four Seasons’ model of summer (December-February), autumn (March-May), winter (June-August), and spring (September-November) to the weather of SWWA (Nind 1831). While reporting of almost every botanical investigation undertaken in the SWBP/SWWA has a comment about the region’s Mediterranean climate, only a few publications
make mention of the four seasons applied by the general public (Rippey 1995; E.A. George 2002; Hussey and Wallace 2003). However, over the past 40 years numerous studies found significant evidence to support the four season model (Gentilli 1971, cited in Western Australia. IOCI Panel 2002; P.B. Wright 1974; Allan and Haylock 1993; Nicholls et al. 2001). These studies investigate climate metrics such as terrestrial air temperatures, precipitation patterns, and sea surface temperatures.

As the first human arrivals in SWWA, the Noongar people have resided in the SWBP for the past 40,000-50,000 years (Flood 1995; Bindon 1997; Gole 2006). Many of the Noongar creations stories begin “Long before the nyitting (sometimes nydiny) ...” or “In the nyitting ...”, which loosely translates as “Before/In the cold dark times long ago” (Morrison et al. 1993, quoted in Wallace and Huston 1997; Nannup and Deeley 2006). This living oral history is a record of the cooling experienced in SWWA/Bibbulman Country during the last ice age 14,000-20,000 years ago (Australia. Bureau of Metrology 2010). As the last Ice Age abated and temperatures began to rise, the Noongar people moved across the landscape in response to the rhythm of the six seasons (Table A) that emerged in SWWA (Harben and Collard n.d.; Wallace and Huston 1997; Australia. Bureau of Meteorology 2010).

**Table A:** The Six Noongar Season (Adapted from Harben and Collard n.d.; Bindon and Walley 1992; Murdoch University 2008).

<table>
<thead>
<tr>
<th>Noongar Season</th>
<th>Approximate Timing</th>
<th>Character of the Season</th>
</tr>
</thead>
<tbody>
<tr>
<td>Birak</td>
<td>Dec-Jan</td>
<td><strong>First Summer. Season of the Young.</strong> Reptiles emerge from hibernation. Hot &amp; dry time with easterly winds during the day and cooler south-westerly sea breeze during late afternoon.</td>
</tr>
<tr>
<td>Bunurua</td>
<td>Feb-March</td>
<td><strong>Second Summer. Season of Adolescence.</strong> Children learn the art of tool-making. Hot easterly and north winds. Fishing &amp; hunting coincide. Large sections of the country were abandoned for lack of water.</td>
</tr>
<tr>
<td>Djeran</td>
<td>April-May</td>
<td><strong>The Autumn. Season of Adulthood. Time of marriages &amp; courtship ceremonies.</strong> Becoming cooler with winds from southwest.</td>
</tr>
<tr>
<td>Makuru</td>
<td>June-July</td>
<td><strong>The First Rains. Fertility Season. Time to travel to inland hunting areas.</strong> Cold &amp; wet weather with westerly gales.</td>
</tr>
<tr>
<td>Kambarang</td>
<td>Oct-Nov</td>
<td><strong>The Wildflower Season. Season of Birth.</strong> Carpets of wildflowers. Receding rain. Small family parties’ link together and larger groups started moving towards the coast.</td>
</tr>
</tbody>
</table>
The progression of the Noongar seasons from the first rains of Makuru to Djilba and on into Kambarang with its receding rain, aligns with the previously mentioned observations of Wells (1884, quoted in IOCI Panel 2002), P.B. Wright (1974), and Allan and Haylock (1993), all of whom reported that generally most rainfall occurs in the early months of the wet season, with August to October being dryer.
Chapter 3: Methodology

3.1 Field Survey Site

Typical of the numerous short range endemics for which the Southwest Botanical Province is renowned, the distribution of *Verticordia staminosa* subsp. *staminosa* (Figure 1) is restricted to crevices in the granite pavement on the upper slopes of a single inselberg approximately 10km northeast of the wheatbelt town of Wongan Hills (Withers 2000; Hopper and Gioia 2004; Yates and Ladd 2004).

One of the six regions around the planet which are described as having a classically Mediterranean climate, the SWBP experiences warm dry summers and cool wetter winters (Australia. Bureau of Meteorology (BoM) 2011; Cowling et al. 2005; Yates and Ladd 2004). However, the Noongar people of south-western Australia recognise six seasons within this region (Australia. Department of Environment and Heritage 2006; Western Australia. Department of Water 2011). BoM (2011) weather observations from the Wongan Hills township provide the nearest verified and analysable climate data (Table B) for *Verticordia staminosa* subsp. *staminosa*.

**Figure 1:** Location of *V. staminosa* populations adapted from Gioia 2007 and Geoscience Australia 2009.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Annual Mean</th>
<th>Monthly Mean Summer (Nov-April) (Mean ± 95% CI)</th>
<th>Monthly Mean Winter (May-Oct) (Mean ± 95% CI)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum Temp.</td>
<td>25.7 °C</td>
<td>31.2 ± 2.4 °C</td>
<td>20.1 ± 2.4 °C</td>
</tr>
<tr>
<td>Minimum Temp.</td>
<td>11.9 °C</td>
<td>15.7 ± 1.7 °C</td>
<td>8.2 ± 1.2 °C</td>
</tr>
<tr>
<td>Diurnal Variation</td>
<td>13.7 °C</td>
<td>15.5 ± 1.2 °C</td>
<td>11.9 ± 1.5 °C</td>
</tr>
<tr>
<td>Rainfall</td>
<td>391.4 mm</td>
<td>17.7 ± 2.8 mm</td>
<td>47.4 ± 15 mm</td>
</tr>
<tr>
<td>Rainy Days</td>
<td>87.6</td>
<td>3.4 ± 0.8</td>
<td>11.2 ± 2.6</td>
</tr>
<tr>
<td>Daily Solar Exposure</td>
<td>20.1 MJm⁻²</td>
<td>25.0 ± 4.1 MJm⁻²</td>
<td>15.1 ± 4.1 MJm⁻²</td>
</tr>
<tr>
<td>Daily Evaporation*</td>
<td>6.2 mm</td>
<td>9.0 ± 1.7 mm</td>
<td>3.4 ± 1.1 mm</td>
</tr>
</tbody>
</table>
3.2 Study Species

*Verticordia staminosa* subsp. *staminosa* is a naturally rare sclerophyllous Myrtaceae shrub which grows in a single meta-population of approximately 1 300 plants distributed across 49 largely unconnected subpopulations (E.A. George 2002; Yates and Ladd 2004; Hopper 2009). Approximately 400 kilometres (Figure 1) and an estimated 1.0-1.5 million years of evolution separates subspecies *staminosa* from its closest relatives, two varieties of the equally rare subspecies *cylindracea* that grow in several disjunct populations on granite outcrops in the Newdegate/Lake King area (A.S. George 1991; E.A. George 2002; Patten et al. 2004; Yates and Ladd 2004).

During the winter wet season (May-Oct) the one to several basal stems of a reproductive *Verticordia staminosa* subsp. *staminosa* plant support a dense low (0.3-0.6 metres) spreading (0.6-1.0 metres) bright green canopy of narrow almost stalkless leaves and many yellow-green to reddish-brown pendulous hermaphroditic non-autogamous flowers that hang under the foliage (A.S. George 1991; E.A. George 2002; Yates and Ladd 2004). All three forms of *V. staminosa* become dormant to avoid the summer drought (E.A. George 2002; A.S. George 2002; Yates et al. 2007). After rain they recover from a brown mostly leafless and, in some cases collapsed state, with the retained foliage rapidly greening and by producing “small, vigorous tufts of new regrowth on old branches” (Patten et al. 2004; Yates and Ladd 2004). Having no lignotuber, *Verticordia staminosa* is generally considered to be a fire sensitive species (E.A. George 2002; Patten et al. 2004; Yates et al. 2007).

*Verticordia staminosa* is a surplus flower producer with low seed set, approximately one in three flowers develops a single viable seed (Yates and Ladd 2004), although a few pericarps contain a second viable seed. It has been suggested that this relative low cost strategy provides an ovary reserve as a buffer against flower mortality caused by adverse weather conditions and/or allows such species to increase germination and establishment rates in seasons with especially favourable environmental conditions (Cochrane et al. 2001; Yates and Ladd 2004).

An increase in germination of *V. staminosa* seedlings was observed in a year when the rainfall was substantially greater than the long term average (Yates and Ladd 2004). Seedlings of all three forms of *Verticordia staminosa* have been
observed to germinate in cracks in the pavement, moss mats, and/or shallow pockets of soil (E.A. George 2002; Patten et al. 2004; Yates and Ladd 2004; Yates et al. 2007). However for *Verticordia staminosa* subsp. *staminosa*, only those seedlings that germinate in a crevice survive the first summer (Yates and Ladd 2004; Yates et al. 2007).

### 3.3 Seed Viability of the Soil Seed Bank

During a site visit in winter of 2008, Dr Colin Yates from the Science Division of the Department of Environment and Conservation (formerly within the Department of Conservation and Land Management) and Dr Philip Ladd from the Murdoch University School of Environmental Science collected a random representative sample of pericarps from under reproductive plants within several subpopulations in the vicinity of monitored subpopulations, which they aggregated into a well mixed composite sample. I randomly selected three sets of 40 pericarps from the composite sample and carried out a ‘Cut Seed Test’ to determine which pericarp contained a viable seed (Moles et al. 2003; Turner 2005). I removed the sepals and petals from the selected pericarp by brushing them over a stainless-steel 100μm mesh, weighing them on an analytical balance, and then cutting the pericarps in half to determine how many contained a plump white embryo. My method for statistically analysing the outcome of this Cut Test is detailed in Section 3.8.3.

### 3.4 Selection and Preparation of Germination Containers

For all my germination experiments I randomly selected the most appropriate matched set of punnets, seedling pots, and/or trays from glasshouse stock; thoroughly cleaned the containers in fresh chlorinated water; sterilised them in 1% hypochlorite solution; rinsed the containers in deionised water; and then let them air dry at 65°C for 45 minutes. Under hygienic conditions I marked each pot with a unique code that identified the container and any treatment applied. To simulate the mineral soils of crevices in the granite pavement on Mocardy Hill, I filled each container with washed river sharp sand supplemented with a proprietary slow release fertiliser formulated for Australian native plants.

### 3.5 Longevity of Seed Viability

The experimental design for soil storage of pericarps to determine the longevity of seed viability was developed and implemented by Dr Yates and Dr Ladd. The detail for actions performed prior to my participation in both the annual
V. staminosa demographic surveys from 2007 and recovering buried samples of pericarps in late 2009 are based on my personal communications with Dr Ladd and Dr Yates during the period 2007-2011. In 2001 a random representative sample of pericarps collected from under reproductive plants growing in several subpopulations in the vicinity of monitored subpopulations, were aggregated into a well mixed composite sample, and then 54 sets of 100 fruit were randomly selected from the composite sample. Half the sets of pericarps were randomly selected for burial in cracks within a single subpopulation and the other half for burial in soil aprons adjacent to the same subpopulation, which were in part covered by mosses. The sets of pericarps were mixed with washed river sharp sand and stitched into free draining nylon bags of 20cmx2cm for burial in cracks or 10cmx10cm for burial in the soil aprons.

The wider section of three unmonitored cracks in the granite pavement at subpopulation H were excavated to a depth of approximately 5cm, the nylon bags were tamped into position, the crack was backfilled with excavated material, and wire stakes with plastic tags were used to mark the location of the sample bags. In three aprons of soil congruent to subpopulation H, stakes were driven into the ground in 3mx3m matrices and the sample bags buried to a depth of 5cm at 1m spacing within each grid. The original experimental design involved recovering a randomly selected subset of nine sample bags from the cracks and three sample bags from each soil apron at intervals of one, two, and three years after burial to characterise longevity of seeds in the soil seed bank. However this did not occur. In the spring of 2009 Dr Ladd and I recovered all the bagged samples (hereafter replicates) that we could locate.

Using a binocular dissection microscope and tweezers, I removed all complete and fragmented pericarps from the washed river sand and root material contained in each recovered replicate. To demonstrate that none of the seeds remained viable, I planted all the visually desiccated and weathered pericarps (complete and fragmented) into 30 individual matched pots. Without replication, I planted all pericarps in a replicate into an individual pot and watered them daily with deionised water in an attempt not to produce seedlings. My experimental balance is shown in Table C and my approach for statistically analysing the unexpected emergence of seedlings appears in Section 3.8.4.

Table C: Experiment Balance.

<table>
<thead>
<tr>
<th>Recovered Replicates (Samples)</th>
<th>Crack</th>
<th>Soil Apron</th>
</tr>
</thead>
<tbody>
<tr>
<td>13</td>
<td>17</td>
<td></td>
</tr>
</tbody>
</table>
3.6 Impact of Smoke and Weathering on Germination

To investigate the impact of smoke on the germination of *V. staminosa* seeds I performed the following fully randomised and balanced experiment to examine both number of seedlings that emerged and the time taken for seedlings to emerge. For this experiment I decided that the four treatments should be weathering the pericarps, weathering and smoke treating the pericarps, exposing the pericarps to smoke, and a control group. I randomly selected 360 individual seedling pots and ten seedling trays from glasshouse stocks and pre-treated these by the method detailed in Section 3.4.

I randomly selected pericarps from the composite representative sample collected by Dr Yates and Dr Ladd, removed petals and sepals by the method described in Section 3.3, and weighed them to identify pericarps which were likely (α=0.05) to contain a viable seed. From this batch of 500 pericarps I concurrently and randomly selected four sub-samples of 90 pericarps each.

I randomly selected two sub-samples of 90 pericarps for artificial ‘weathering’. Adapting techniques from the literature on artificially hydro-priming/weathering fruits/seeds, I performed 30 repetitions of agitating and soaking the sub-samples in deionised water for one hour and then air drying them in a thermostat controlled oven at 30°C (to avoid heat-shocking the seeds) for two hours (Leopold 1964; Mott 1974, Merritt et al. 2007; Cousens et al. 2010). Following the instructions for the aqueous smoke treatment I obtained from Kings Park and Botanic Garden, I randomly selected one of the weathered sub-samples and one of the unweathered sub-samples soaked each in a mixture of the smoke treatment and deionised water for one hour prior to planting. To keep the number of treatments consistent, I also soaked the remaining two sub-samples in deionised water for one hour. After planting all the individual pericarp into the pots, I randomly assigned nine pots of each treatment to each of the ten seedling trays in a 6x6 matrix. The experimental balance is given in Table D.

Conducting this experiment during winter in Perth, which has a Mediterranean climate similar to Wongan Hills, I placed the ten full trays on a single bench in Murdoch University’s Glasshouse 2. I inspected the experiment each evening and for every new seedling I again recorded the number of days since planting, pot identification, tray number, and treatment until four weeks after the last seeding emerged. Every second day I watered the pots with deionised water and
randomly repositioned every tray on the bench to minimise the possibility of tray position confounding the outcome of the experiment. My approach to statistically analysing the outcomes of this experiment is detailed in Section 3.8.5.

**Table D:** Balance of the Glasshouse Experiment with Four Treatments

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Smoke and Weathering</th>
<th>Treatments</th>
<th>Smoke</th>
<th>Weathering</th>
<th>Control</th>
<th>Total Fruit in Tray</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tray 1</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>36</td>
</tr>
<tr>
<td>Tray 2</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>36</td>
</tr>
<tr>
<td>Tray 3</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>36</td>
</tr>
<tr>
<td>Tray 4</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>36</td>
</tr>
<tr>
<td>Tray 5</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>36</td>
</tr>
<tr>
<td>Tray 6</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>36</td>
</tr>
<tr>
<td>Tray 7</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>36</td>
</tr>
<tr>
<td>Tray 8</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>36</td>
</tr>
<tr>
<td>Tray 9</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>36</td>
</tr>
<tr>
<td>Tray 10</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>36</td>
</tr>
<tr>
<td><strong>Total Fruit in Treatment</strong></td>
<td>90</td>
<td>90</td>
<td>90</td>
<td>90</td>
<td>90</td>
<td>360</td>
</tr>
</tbody>
</table>

### 3.7 Germination Field Surveys

As with the longevity of seedling viability discussed above, the experimental design for collecting the field data I analysed was developed and implemented by Dr Yates in collaboration with Dr Ladd.

In winter of the anomalously wet year of 1999 (England et al. 2006; Nicholls, et al. 2001), between nine and fifteen 1mx1m quadrats were established in each of four subpopulations (A, B, G, and W) of *V. staminosa* (Table E). The quadrats were positioned to be representative of the subpopulation, but all were positioned to contain at least one crack that contained seedlings and where possible they also contained a section of moss mat with seedlings. In spring of subsequent years, except 2004 when Dr Ladd was on sabbatical, the number of seedlings surviving from the previous year and the number of new seedlings has been recorded for cracks and moss mat within each quadrat. I have participated in these seedling surveys since spring 2007.

**Table E:** Balance for Field Germination Experiments.

<table>
<thead>
<tr>
<th>Number of Quadrats</th>
<th>Subpopulation A</th>
<th>Subpopulation B</th>
<th>Subpopulation G</th>
<th>Subpopulation W</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>10</td>
<td>9</td>
<td>13</td>
<td>15</td>
</tr>
</tbody>
</table>
My consolidation of the field records produced an analysable data set for field germination covering 11 years with 47 replicates distributed across four subpopulations for germination.

3.8 Statistical Analysis

3.8.1 General Approach to Statistical Analysis

Unless I state otherwise, all descriptive statistics in my thesis are reported as the mean ± 95% confidence interval for the metric in question. Due to the relatively small sample sizes in my experiments, I calculated 95% confidence intervals by determining the value of the t-statistic for the appropriate degrees of freedom and applied the calculation in Box 1 (Berenson et al. 2006).

\[
\mu \pm t_{\text{critical}} \times \text{Standard Error} = \mu \pm t_{\text{critical}} \times \frac{\text{Standard Deviation}}{\sqrt{\text{Sample Size} (n)}}
\]

Such that \( P(t_{0.05,(n-1)} \leq t_{\text{critical}}) = 0.975 \) (Upper tail area = \( 0.05/2 = 0.025 \))

Box 1: Calculating the 95% Confidence Interval.

I performed an exploratory analysis for data from all experiments by graphing histograms and Box & Whisker Plots (Fig. 2). For data that was normally distributed or could be normalised, I graphed means with 95% confidence intervals and tested hypotheses using parametric tests, such as the \( t \)-test and two-way ANOVA (Berenson et al. 2006).

Due to the binomial nature of the field and glasshouse experiments (i.e. seedling present/not present), there were a high number of ‘0’ results generated by seedlings not emerging in all experiments. This prevented this data being normalised by any means, including the Log(x+1) transformation. To test hypotheses about relationships for these data sets, including the impact of climatic variables, I used logistical regression techniques. This application of the General Linear Model makes no assumptions about the nature of predictor variables (i.e. categorical/factor or covariate) or how they are distributed (Berenson et al. 2006; Johnson and Wichern 2002; Tabachnick and Fidell 1996). Predictor variables (or the associated residuals) do not have to be normally
distributed, linearly related, or of equal variance in each group (Tabachnick and Fidell 1996). Also, unlike analyses based on the normal distribution, or approximations to it, logistical regression does not assume that predictor values of less than zero have positive probabilities (Tabachnick and Fidell 1996; Hillborn and Mangel 1997). Juliano (1993) recommends logistical regression for investigating survivorship “under different, naturally occurring conditions”.

I performed all exploratory data analysis and parametric statistical testing using Microsoft® Excel 2003 (Microsoft Corporation 2002) and I used Minitab 15.0 (Minitab 2007) for the logistical regression analyses.

3.8.2 Interpretation of Logistical Regression

In the first instance, I assessed the overall significance of each logistical regression model by examining the Log-Likelihood for a model to determine if it was significantly different from Null Effect or Constant Model, which is applicable if none of the hypothesised predictors significantly affects the outcome of an experiment. I also assessed the quality of the model through the use of Delta Pearson χ² plots for event probability and the leverage of each factor/covariate pattern (Berenson et al. 2006; Tabachnck and Fidell 1996; Mintab 2007).

In developing ‘model webs’ to explore the significance of hypothesised predictor terms and their relationship to other predictors I used the calculation in Box 2 to determine the ranking of nested Models (Tabachnck and Fidell 1996).

\[
\chi^2 = 2[(\text{log-likelihood for larger model}) - (\text{log-likelihood for smaller model})]
\]
\[
df = (\text{number of Predictors in larger model}) - (\text{number of Predictors in smaller model})
\]

Box 2: Calculating χ² to compare nested Models.

In the example model web shown in Figure 3, where the χ² \text{Test} value is greater than the χ² \text{Critical} value the larger model is superior and the term absent from the smaller model is a significant predictor (i.e. P-value <0.05). This is illustrated by the arrow pointing to the superior model. If none of the terms assessed by the logistical regression is a significant predictor of the outcome (i.e. P-values >0.05), then the null or constant model applies. Care needs to be taken when interpreting P-values≈0.05 (0.03-0.06), as illustrated by the double ended arrow in the top left of the Model Web (Berenson et al. 2006). The odds ratio is calculated by dividing the probability of a success by the probability of failure, that is odds ratio = P(Success)/(1-P(Success)). For this example Predictor 2 is significant and the optimum model is \(\ln(\text{odds ratio}) = \text{constant} + \beta_1\text{Predictor 2}\).
When performing stepwise logistical regression to model the impact of climatic variables on germination and seedling survival in the first year, I also considered the individual $Z$-scores, $P$-values, and odds ratios for each predictor. I utilised the Deviance statistic, which measures the fit of a hypothesised model compared to the fit of the saturated model, to assess the predictive ability of models with multiple predictors (Berenson et al. 2006).

### 3.8.3 Seed Viability of the Soil Seed Bank

Sample sizes for this experiment were relatively small, especially in relation to the number of pericarps that contained a viable seed, however my exploratory data analysis suggests, although slightly skewed, the distribution of pericarps with and without a viable seed is approximately bell-shaped (Appendix A2.1). I therefore applied the Central Limit Theorem and assumed that means and proportions of values determined for each trial approximate either a normal distribution $N(\mu, \sigma^2)$ or binomial approximation to the normal distribution $N(np, np(1-p))$ respectively (Berenson et al. 2006).

I determined the mean mass of pericarp with and without viable seeds, and calculated the 95% and 99% confidence level for both means. From this analysis I determined that selecting cleaned pericarp with a mass of greater than 7.5 mg maximised the likelihood that pericarps used in germination trials contained a
viable seed (Section 4.2). I used the Chi-Square ($\chi^2$) Test for difference between more than two proportions to compare the number of pericarps with viable seeds across the three trials (Berenson et al. 2006). With no difference between the proportions for the individual trials (see Section 4.2), I combined the data for the three trials to calculate the overall proportion of pericarps that contain a viable seed, the standard error, and the 95% confidence interval for the proportion using the calculations shown in Box 3 (Berenson et al. 2006).

### Box 3: Calculating the Standard Error and the 95% Confidence Interval

$$\text{Proportion (} p \text{) } \pm \text{ t}_{0.05,2} \times \text{ Standard Error}$$

$$= p \pm \text{ t}_{0.05,2} \times \sqrt{\frac{p(1-p)}{\text{Sample Size (n)}}}$$

where $\text{t}_{0.05,2} = 1.9799$

3.8.4 Longevity of Seed Viability

As I expected, exploratory data analyses suggest that the number of seedlings emerging in replicates recovered from cracks or soil aprons follows a Poisson distribution (Appendix A2.2) and cannot be analysed by parametric statistical tests. However, the time taken for seedlings to emerge in recovered replicates loosely approximated a normal distribution. Given its robustness and the sample size involved, I used the t-Test for common variances to test the null hypothesis of no difference in the mean emergence time (Berenson et. al. 2006).

For the purpose of this analysis I assumed the initial seed viability of the buried pericarps was 32.5% (justified in Section 4.2). I multiplied the number of recovered pericarps from each replicate by this proportion to determine the ‘original viability’ for each replicate and then calculated the proportion of seedlings that emerged. While the data set was relatively small, my exploratory data analyses suggested this binomially distributed data also provided a reasonable approximation to the normal distribution, that is follow a bell-shaped curve (Berenson et. al. 2005). However, the combination of small sample sizes and an apparent bias toward seeds no longer being viable meant that I could not apply the test of two proportions based on the normal approximation to the binomial distribution, so I used the Chi-Square Test for Proportionality to investigate the null hypothesis that burial location was not a factor that impacted long term seed viability (Moore and McCabe 1993; Berenson et al. 2006). Having obtained indicative results from the $\chi^2$ Test, I further investigated the veracity of my findings by applying a statistically more powerful and robust logistical regression analysis (Tabachnck and Fidell 1996).
3.8.5 Impact of Smoke and Weathering on Germination

My exploratory data analyses show a high degree of variability and skew in the distributions for both the number of seedlings that emerged and the time it took seedlings to emerge. With no viable transforms for normalising the data, I applied logistical regression to determine if any relationships exist in relation to the dormancy breaking treatments (i.e. smoke and/or weathering) and/or the experimental design (i.e. Tray effect). The outcomes of the exploratory data analyses and the Logistical Regression are given in Section 4.4.

3.8.6 Analyses for Climate Data

From the Australian Bureau of Meteorology (2011) Climate Data Online I obtained daily observations from the Wongan Hills Meteorological Station (Station 008137) for precipitation (hereafter rainfall), maximum and minimum temperatures, and solar radiation from 1991 to 2010. From these values I calculated the key metrics for germination (Section 2.4.1) listed in Table F.

Table F: Calculation of climate metrics shown to impact germination & seedling survival.

<table>
<thead>
<tr>
<th>Metric</th>
<th>Method of Calculation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rainfall (mm)</td>
<td>Total rainfall recorded for the calendar year (annual rainfall) or season.</td>
</tr>
<tr>
<td>Number of Rainy Days</td>
<td>Number of days in the calendar year or season when recorded rainfall was greater than or equal to 1mm.</td>
</tr>
<tr>
<td>Rainfall Intensity (mm)</td>
<td>Usually amount of rainfall per event, but here calculated as Average Rainfall per Rainy Day.</td>
</tr>
<tr>
<td>Average Monthly Solar Radiation (MegaJoules per square metre – MJ/m²)</td>
<td>Average of the Monthly Averages across the period of interest (i.e. annual or season). Monthly Averages calculated by averaging the incident solar radiation for each day of each calendar month.</td>
</tr>
<tr>
<td>Average Monthly Maximum Temperature (Celsius – °C)</td>
<td>Maximum daily temperatures were averaged within each calendar month and means of these Monthly Averages are calculated for the periods of interest.</td>
</tr>
<tr>
<td>Average Monthly Minimum Temperature (Celsius – °C)</td>
<td>Minimum daily temperatures were averaged within each calendar month and the means of these Monthly Averages were calculated for the periods of interest.</td>
</tr>
<tr>
<td>Average Monthly Temperature (Celsius – °C)</td>
<td>Daily Average Temperatures were calculated by averaging the Maximum and Minimum Temperature for each day. These values were averaged within each calendar month and the means of these Monthly Averages were calculated for the periods of interest.</td>
</tr>
<tr>
<td>Average Monthly Diurnal Temperature Range (Celsius – °C)</td>
<td>Each day’s Minimum Temperature was subtracted from the Maximum. These values were averaged within each calendar month and the means of these Monthly Averages were calculated for each period.</td>
</tr>
</tbody>
</table>
I use these metrics to investigate relationships for the weather of this 20 year period in terms of the annual cycle and the three types of seasons (Section 2.4.2) that have been observed to operate in the SWBP.

Initially I used histograms and Box & Whisker Plots to investigate variability between annual weather cycles and to look for evidence of the three season models reported to operate in the SWBP, which is a Mediterranean climate (Dry Season/Wet Season); the traditional Four Seasons of summer, autumn, winter, and spring; and the Six Noongar Seasons. My analyses revealed that all the annual climate metrics provided a reasonable approximation to the normal distribution. This allowed me to assess inter-year variability by comparing the annual values of each metric to its long-term (1991-2010) mean using a Chi-Squared Analysis (Berenson et al. 2006). At the finer season scale there was a high degree of variability and highly skewed distributions for the rainfall related metrics, however the solar radiation and temperature based metrics were distributed as a reasonable approximation to the normal distribution (Appendix C). This being the case I utilised t-Tests for uncommon variance, which are sufficiently robust to deal with skewed data, to analyse between season variability for the three rainfall metrics under a Mediterranean climate (Berenson et al. 2006). These analyses revealed significant inter-seasonal variation for all three metrics (Section 4.5.2) and as the distributions for these metrics under the other two season models were similarly skewed, I assume the inter-seasonal variation to be significant for all three types of seasons. With the solar radiation and temperature metrics approximating normal distributions for all season models, I utilised two-way ANOVAs without repetition to investigate the significance of inter-season and inter-year variability for these metrics. I used bi-variate least-squares linear regression to investigate collinearity between those metrics within each season that approximated a normal distribution (Philippi 1993). The outcomes of these analyses are all reported in Section 4.5.

3.8.7 Impact of Climatic Variables on Germination in the Field

Given that *V. staminosa* has been present on granite outcrops in the Wongan Hills area for at least the past 1.5 million years and the highly restricted range of the extant meta-population, I assumed that competition and edaphic variables were largely constant over the restricted geographic and temporal range within which the data I analyse was collected (Gardner 1959; Hopper and Gioia 2004; Yates and Ladd 2004; Yates et al. 2007; Hopper 2009).
Yet again my exploratory data analyses revealed that parametric techniques are not suitable for analysing field germination. I investigated the presence of any significant relationships by using logistical regression (Section 4.5). I analysed this experiment by developing webs of models and applying Stepwise Logistical Regression, with guidance from the correlation analysis described in Section 3.8.6, to ascertain how various climate metrics may have influenced germination of \textit{V. staminosa} seedlings in crevices within the granite pavement at Mocardy Hill since 1999 (Tabachnck and Fidell 1996; Ramsey and Schafer 2002).

These logistical regressions produced a suite of models for the influence of climatic factors on the germination of \textit{V. staminosa} seedlings under a Mediterranean climate, the tradition four seasons, and the six Noongar seasons. I applied Burnham and Anderson’s (2002) approach to Akaike’s Information Criterion (1973; cited in Burnham and Anderson 2002) to ranking statistical models. This allowed me to identify a ‘top model’ from the suite of germination models, and to explore the strength of evidence provided by lesser models in comparison to the top model. The calculations for Akaike’s Information Criterion (AIC) are given in Box 4. The outcome of this ranking process is reported in Section 4.6.5

<table>
<thead>
<tr>
<th>Akaike’s Information Criterion (AIC)</th>
<th>Model Probabilities ($\omega_i$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\text{AIC} = -2 \text{Log-likelihood} + 2K$</td>
<td>$\omega_i = \frac{\exp(-\frac{1}{2} \Delta_i)}{\sum \exp(-\frac{1}{2} \Delta_i)}$</td>
</tr>
</tbody>
</table>

Where $K$ is the sum of the number of terms for the intercepts, the variances, and the predictors.

AIC Differences ($\Delta_i$)

$\Delta_i = \text{AIC}_i - \text{AIC}_{\text{min}}$

Best model (i.e. lowest Log-likelihood) has $\Delta_i \equiv \Delta_{\text{min}} \equiv 0$.

**Box 4:** Burnham and Anderson’s (2002) approach to calculating AIC values.
Chapter 4: Results

4.1 Exploratory Data Analyses

My exploratory data analyses using Histograms and Box & Whisker Plots revealed that many of my raw data sets were skewed and only a few approximated the “bell-shaped” curve of the normal distribution (Appendices A-C).

4.1.1 Data Sets that Approximate a Normal Distribution

From the field and glasshouse germination experiments the mass of pericarp with and without viable seed, the time taken for seedlings to emerge, and the proportion of ‘originally viable seeds’ that germinated from the soil stored pericarps generally approximated the normal distribution or could be normalised. This allowed me to directly analyse those datasets using parametric statistical tests. To compare the mass of pericarps with and without a viable seed, I needed to combine the means of three trials and apply the Central Limit Theorem (Section 3.8.3).

The annual climate metrics all approximated the normal distribution (Appendix C1). However, at the finer seasonal scale only the temperature metrics approximated the normal distribution (Appendices C2 to C4). This outcome is predicted by the Central Limit Theorem as the temperature metrics are determined by sets of sample means.

4.1.2 Data that Can Not Be Normalised by Transformation

Histograms and Box & Whisker Plots for the number of seedlings that emerged in the germination experiments for both the soil buried pericarps and the impact of smoke and weathering on seeds appeared to follow a Poisson distribution rather than the normal distribution (Appendices A2 and A3). Unlike the germination of recovered pericarps experiment, the portions of seedlings that germinated in the smoke and weathering experiment is also highly skewed. Unlike the time taken for seedlings to emerge from the soil stored pericarps, surprisingly the average time taken for seedlings to emerge from the smoke treated and weathered pericarps (i.e. for each treatment in a tray) was also too skewed to analyse directly.

To investigate variability of seedling germination between years I investigated if a survey quadrat contained seedlings (i.e. presence/absence), the proportion of quadrats in a subpopulation that contained seedlings, and the average number of seedlings per quadrat within each subpopulation (Appendix B). These
exploratory analyses reveal that the distribution of data for all three metrics is highly skewed. This is even the case for the distribution of sample means for the number of seedlings, which I had expected to be normally distributed in accordance with the Central Limit Theorem.

The skew in these data sets is so great that even after Log transformation they do not approximate a normal distribution, so I did not conduct further parametric analyses on these metrics.

### 4.2 Seed Viability of Soil Seed Bank

After applying the Central Limit Theorem (Section 3.8.3) to smooth and normalise the data from each of the three trails, I calculated the means and associated 95% and 99% confidence intervals for pericarps containing a viable seed and those that did not (Figure 4). From this analysis I decided that selecting cleaned pericarps with a mass of greater than 7.5 mg maximised the likelihood that fruit used in my germination experiments contained a viable seed.

![Figure 4: Mean mass (± 95% & 99% confidence intervals (CI)) of pericarp with and without a viable seed and overall seed viability (± SE & 95% CI).](image)

Assuming that the masses of cleaned pericarps with and without a viable seed approximated the normal distributions $N(8.0 \, \text{mg}, 0.2 \, \text{mg})$ and $N(5.5 \, \text{mg}, 0.4 \, \text{mg})$ respectively, then the probability that I planted a pericarp without a viable seed $P(X \geq 7.5 \, \text{mg})$ was very small ($3.0 \times 10^{-7}$).

With approximately one in three pericarps in each of the three trails containing a viable seed, it was not surprising that the proportions of viable seeds I found in each of the 3 trails were not significantly different from each other ($\chi^2 = 0.926$,
p-value = 0.630, DF = 2). My estimate of 32.5 ± 0.2% (p ± Std Error) for the overall proportion of pericarps that contained a viable seed is in good agreement with the values (mean ± SE) of 32.0 ± 6.1% obtained by Cochrane et al. (2001) and the 3 trials by Yates et al. (2007) which produced values (mean ± SE) of 39.92 ± 2.42%, 35.50 ± 2.64%, and 30.59 ± 2.18%.

### 4.3 Germination Response of Recovered Pericarp

Applying the statistically robust t-Test (Section 3.8.4) to compare the time for seedlings to emerge from the recovered pericarps provides strong evidence (t = 1.655, P-value = 0.562, DF = 146) that there is no difference in the average time for seedlings to emerge from pericarps that were buried in the cracks (34.0 ± 0.8 days) and those buried in the soil aprons (34.3 ± 0.8 days).

![Figure 5: Seedling emergence in recovered pericarp replicates](image)

My analysis of the proportion of ‘originally viable’ seeds that produced seedlings (Section 3.8.4), revealed there is not a significant difference in the proportions of seedlings emerging from replicates buried in a crack or from those buried in the soil apron (Table G). There may be a difference between replicates recovered from the cracks and the replicates recovered from the soil apron. However, this result is at odds with the graphical evidence (Figure 5), which is supported by the logistical regression model \[\text{Ln(odds ratio)} = \text{constant} + \beta_1 \text{Crack}\] producing a Log-Likelihood of -334.967 (χ² = 0.997; P-value = 0.318; DF = 1). This provides strong evidence that burial location does not significantly impact seed longevity.

### Table G: Outcomes of Chi-Square Tests for differences between proportions of seedlings within treatments and between treatments (Buried in Cracks or in Soil Aprons).

<table>
<thead>
<tr>
<th></th>
<th>χ² Test Statistic</th>
<th>P-value</th>
<th>Degrees of Freedom</th>
</tr>
</thead>
<tbody>
<tr>
<td>Within Cracks</td>
<td>4.62 x 10⁻¹²²</td>
<td>≈ 1</td>
<td>12</td>
</tr>
<tr>
<td>Within Soil Aprons</td>
<td>5.27 x 10⁻⁶⁷</td>
<td>≈ 1</td>
<td>16</td>
</tr>
<tr>
<td>Between Cracks and Soil Aprons</td>
<td>8.55</td>
<td>0.003</td>
<td>1</td>
</tr>
</tbody>
</table>

The median (and range) for the number and the proportion of originally viable seeds that germinated in each replicate was 3 (0-11) seedlings at 10.2% (0%-35.5%). Normally distributed by the Central Limit Theorem, the mean of the mean emergence time per replicate was 34.8 ± 0.4 days.
4.4 Impact of Smoke and Weathering on Germination

Mintab 15.0 allows categorical data such as the four treatments of Smoke & Weathering, Weathering, Smoke, and Control to be grouped together and modelled under single ‘predictor’ term (e.g. Treatment). Despite having 90 replicates of each treatment, my data set was too small to analyse the interaction between the Tray that a seedling germinated in and the Treatment it received. However, my logistical regression analyses (Figure 6) provides strong evidence that neither predictor is significant, the Constant Model appears the most valid, and it is unlikely that the interaction term (Treatment*Tray) on its own would constitute the “Perfect Model” (Tabachnick and Fidell 1996).

![Logistical Regression Analysis Diagram]

**Figure 6:** Web of models for effect of Tray and Treatment.

The median (and range) for the number and proportion of seedlings emerging in each tray was 21 (17-24) and 58.3% (47.2%-66.7%). Normally distributed by the Central Limit Theorem, the mean emergence time between treatments were not significantly different, but the overall mean emergence time of 45.6 ± 0.7 days is significantly longer than the 34.8 ± 0.4 days for the pericarps recovered from the cracks and soil apron (t=9.48; P-value<<0.001; DF = 10 & 12 respectively).

4.5 The Seasons of South-West Western Australia

Exploratory data analyses outlined in Section 4.1 provides evidence that the Mediterranean style Dry and Wet seasons; the four seasons of summer, autumn, winter, and spring; and the six Noongar seasons apply in the Wongan Hills area.
4.5.1 Annual Climate Metrics

Chi-Squared analyses of the annual means of each metric against the 20 year (1991-2010) long-term mean value revealed that annual rainfall and the number of rainy days were the only metrics with significant between year variability (Table H).

**Table H:** Outcomes of Chi-Square Tests for difference between annual values and the 20 year (1991-2010) long-term averages for key climate metrics.

<table>
<thead>
<tr>
<th>Metric</th>
<th>Statistics</th>
<th>Metric</th>
<th>Statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annual Rainfall</td>
<td>$\chi^2 &gt;&gt; 50$\n</td>
<td></td>
<td>P-value $&lt;&lt; 0.001$</td>
</tr>
<tr>
<td>Annual Rainy Days</td>
<td>$\chi^2 = 40.75$\n</td>
<td></td>
<td>P-value $= 0.002$</td>
</tr>
<tr>
<td>Annual Intensity</td>
<td>$\chi^2 = 2.226$\n</td>
<td></td>
<td>P-value $\approx 1.000$</td>
</tr>
<tr>
<td>Annual Avg Monthly Solar Radiation</td>
<td>$\chi^2 = 0.736$\n</td>
<td></td>
<td>P-value $\approx 1$</td>
</tr>
</tbody>
</table>

Not unexpectedly amount of Annual Rainfall and the number of rainy days are very highly correlated ($R^2 = 61.8\%$; $F = 29.06$; P-value $= <0.001$). Annual intensity of rain is not correlated to the number of rainy days and is only weakly correlated to annual rainfall ($R^2 = 28.1\%$; $F = 7.046$; P-value $= 0.016$). However I applied Chatterjee and Price’s (1991, quoted in Philippi 1993) axiom that an F-value of greater than 10 “is ... a signal that the data have collinearity problems”, meaning this weak correlation between annual rainfall and Annual intensity is not significant. Also as might be expected, there is a high degree of cross correlation for solar radiation and the four temperature metrics (Appendix D). Somewhat surprisingly annual monthly average maximum temperatures are only collinear with the solar radiation metric.

The high degree of cross correlation of diurnal temperature variation with solar radiation, average monthly temperatures, and minium temperatures and the low cross correlation of the maximum temperature metric, combined with the fact that those two metrics (i.e. diurnal temperature variation and maximum temperature) have been shown to impact germination (Section 2.7.1), I investigated these two metrics and disregarded solar radiation (Section 4.6.1).
4.5.2 Mediterranean (Dry and Wet Season) Metrics

As previously mentioned, the rain metrics for the Dry and Wet seasons are skewed (Appendix C2). Skewed distributions such as these, which can not be assessed by parametric methods, are indicative of outliers and indicate a high degree of variability (Tabachnick & Fidell 1996), in this case inter-year variability. With only two data sets, I was able to compare inter-season variability using the robust t-Test for uncommon variance (Section 3.8.6). I discovered that there is significant difference between seasons for the three rain related metrics (Table J).

**Table J:** Outcomes of t-Test with uncommon variance of between seasons.

<table>
<thead>
<tr>
<th>Rain Metric</th>
<th>t-Statistic</th>
<th>P-values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amount of Rainfall</td>
<td>8.848</td>
<td>&lt;&lt;0.001</td>
</tr>
<tr>
<td>Number of Rainy Days</td>
<td>14.28</td>
<td>&lt;&lt;0.001</td>
</tr>
<tr>
<td>Rain Intensity</td>
<td>2.681</td>
<td>0.014</td>
</tr>
</tbody>
</table>

ANOVA analyses of the temperature and solar radiation metrics (Section 3.8.6) revealed while all the temperature metrics are significantly different between the dry and wet seasons, only diurnal temperature range and solar radiation show significant (P-value <0.05) inter-year variability (Table K). Testing the collinearity of the diurnal temperature range and solar radiation I found a high level of correlation in both the Dry Season ($R^2 = 38.9\%; F = 17.06; P$-value = <0.001) and the Wet Season ($R^2 = 48.7\%; F = 11.49; P$-value = 0.003). Again, as diurnal temperature range impacts germination I investigated this metric further and disregarded the solar radiation (Section 4.6.2).

**Table K:** Variability in the temperature metrics under the Mediterranean Season’s model.

<table>
<thead>
<tr>
<th>Temperature Metric</th>
<th>Inter-season Variability</th>
<th>Inter-year Variability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Solar Radiation</td>
<td>F = 4726</td>
<td>F = 5.194</td>
</tr>
<tr>
<td>Average Monthly Temperature</td>
<td>P-value &lt;&lt;0.001</td>
<td>P-value &lt;0.001</td>
</tr>
<tr>
<td>Average Monthly Maximum Temperatures</td>
<td>F = 1253</td>
<td>F = 1.150</td>
</tr>
<tr>
<td>P-value &lt;&lt;0.001</td>
<td>P-value = 0.381</td>
<td></td>
</tr>
<tr>
<td>Average Monthly Minimum Temperatures</td>
<td>F = 2224</td>
<td>F = 1.550</td>
</tr>
<tr>
<td>P-value &lt;&lt;0.001</td>
<td>P-value = 0.381</td>
<td></td>
</tr>
<tr>
<td>Average Monthly Diurnal Range</td>
<td>F = 385.0</td>
<td>F = 2.689</td>
</tr>
<tr>
<td>P-value &lt;&lt;0.001</td>
<td>P-value = 0.018</td>
<td></td>
</tr>
</tbody>
</table>
4.5.3 Metrics for the Four Seasons Climate

As with the Mediterranean Seasons in the previous section, the rainfall metrics were skewed suggesting a high degree of inter-year variability (Appendix C3). Similarly my ANOVA analyses of the temperature metrics show a significant inter-season variability for all the metrics, but only the diurnal temperature range and solar radiation had significant inter-year variability (Table L). This degree of variability, as a result of extreme (outlier) events, is required to successfully model climatic phenomena (England et al. 2006).

Table L: Variability in the temperature metrics under the Four Season’s model.

<table>
<thead>
<tr>
<th>Temperature Metric</th>
<th>Inter-season Variability</th>
<th>Inter-year Variability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Solar Radiation</td>
<td>F = 4726</td>
<td>F = 4.226</td>
</tr>
<tr>
<td></td>
<td>P-value &lt;&lt;0.001</td>
<td>P-value &lt; 0.001</td>
</tr>
<tr>
<td>Average Monthly Temperature</td>
<td>F = 1140</td>
<td>F = 0.992</td>
</tr>
<tr>
<td></td>
<td>P-value &lt;&lt;0.001</td>
<td>P-value = 0.484</td>
</tr>
<tr>
<td>Average Monthly Maximum</td>
<td>F = 1013</td>
<td>F = 1.601</td>
</tr>
<tr>
<td>Temperatures</td>
<td>P-value &lt;&lt;0.001</td>
<td>P-value = 0.088</td>
</tr>
<tr>
<td>Average Monthly Minimum</td>
<td>F = 751.6</td>
<td>F = 1.392</td>
</tr>
<tr>
<td>Temperatures</td>
<td>P-value &lt;&lt;0.001</td>
<td>P-value = 0.168</td>
</tr>
<tr>
<td>Average Monthly Diurnal</td>
<td>F = 210.7</td>
<td>F = 3.331</td>
</tr>
<tr>
<td>Range</td>
<td>P-value &lt;&lt;0.001</td>
<td>P-value &lt; 0.001</td>
</tr>
</tbody>
</table>

My analyses of the collinearity of the diurnal temperature range and solar radiation metrics also showed a high degree of correlation for Summer ($R^2 = 48.7\%$; $F = 40.81$; P-value < 0.001), Autumn ($R^2 = 41.6\%$; $F = 12.84$; P-value = 0.002), Winter ($R^2 = 39.8\%$; $F = 11.92$; P-value = 0.003), and Spring ($R^2 = 34.5\%$; $F = 9.480$; P-value = 0.006).

4.5.4 Six Noongar Seasons

Similar to both of the previous season models, the rainfall metrics are skewed for the Noongar seasons, which again suggests a high degree of inter-year variability (Appendix C.4). As with my ANOVA analyses for the Mediterranean climate and the traditional four seasons, there is a significant inter-season variability for all the temperature metrics (Table M). A difference with this analysis is that the maximum temperature metric shows significant inter-year variability in addition to the diurnal temperature range and solar radiation metrics. This is the same outcome I observed in my analyses of the annual climate values (Section 4.5.1).
Table M: Variability in the temperature metrics under the Six Noongar Season’s model.

<table>
<thead>
<tr>
<th>Temperature Metric</th>
<th>Inter-season Variability</th>
<th>Inter-year Variability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Solar Radiation</td>
<td>F = 1235</td>
<td>F = 4.303</td>
</tr>
<tr>
<td>P-value &lt;&lt; 0.001</td>
<td>P-value &lt; 0.001</td>
<td></td>
</tr>
<tr>
<td>Average Monthly Temperature</td>
<td>F = 969.2</td>
<td>F = 1.234</td>
</tr>
<tr>
<td>P-value &lt;&lt; 0.001</td>
<td>P-value = 0.249</td>
<td></td>
</tr>
<tr>
<td>Average Monthly Maximum Temperatures</td>
<td>F = 916.7</td>
<td>F = 2.115</td>
</tr>
<tr>
<td>P-value &lt;&lt; 0.001</td>
<td>P-value = 0.009</td>
<td></td>
</tr>
<tr>
<td>Average Monthly Minimum Temperatures</td>
<td>F = 593.8</td>
<td>F = 1.614</td>
</tr>
<tr>
<td>P-value &lt;&lt; 0.001</td>
<td>P-value = 0.068</td>
<td></td>
</tr>
<tr>
<td>Average Monthly Diurnal Range</td>
<td>F = 189.8</td>
<td>F = 4.288</td>
</tr>
<tr>
<td>P-value &lt;&lt; 0.001</td>
<td>P-value &lt; 0.001</td>
<td></td>
</tr>
</tbody>
</table>

Across the six seasons collinearity of the diurnal temperature range, maximum temperature, and solar radiation was highly variable; however there is a significant amount of cross-correlation between these metrics in most seasons (Appendix E). On this basis, I considered the impact of the diurnal temperature range on germination (Section 4.6.4), while disregarding both the maximum temperature and solar radiation metrics with which it is highly correlated.

4.6 Impact of Climatic Variables on Germination in the Field

Because of the relatively small sample size I am unable to determine if there is a difference in germination pattern between quadrats or if the interaction between Subpopulation and Year is significant. However, logistical regression on the presence or absence of seedlings in a quadrat revealed that there is no difference between the four Subpopulations, but year was significant as a factor (Figure 7). Given the strength of the evidence against Subpopulation being a significant predictor, it is reasonable to assume that the interaction term (Subpopulation*Year) is also unlikely to be significant.

Figure 7: Germination models with Subpopulation and Year as factors.
As I found no significant variation in germination between the subpopulations and given the persistence of *V. staminosa* near Wongan Hills for at least the past 1.5 million years, I hypothesise that the difference in germination between years is linked to variability of the weather between seasons. The analyses below explore the impact of climatic variables based on annual values and at the finer scale of two, four, and six seasons.

### 4.6.1 Annual Values

Initially I analysed the impact of climate metrics that I determined to be important in Section 4.5.1 through a standard stepwise logistical regression. This involves a series of iterations that remove the least significant term until only significant predictors remain (Section 3.8.2) producing the optimum model:

\[
\text{Ln(odds ratio)} = 0.650 + 0.001 \text{ Rainfall} + 0.138 \text{ Intensity}.
\]

While this model is significantly better than the null effect model ($\chi^2 = 80.49$; DF = 2; P-Value < 0.001), the constant term is not significant (P-value = 0.847) and the deviance of values predicted by the model from those observed in the field is significant ($H_0$: Model is good fit to data; $\chi^2 = 54.75$; DF = 8; P-Value <0.001). This means that this model is not a good fit to the data and can not be used to make any predictions about germination of *V. staminosa* seedlings in the monitored quadrats.

I created a web of models to further investigate models that may allow the germination of seedlings to be explained by annual values of the climate metrics. This produced two possible models. The first suggested that the number of rain days alone influenced germination, while the second model suggested that a combination of the metrics Rainfall, Rainy Days, Intensity, Cyclones (and tropical lows) and Diurnal Temperature Range influence germination. However, the deviance of predicted values from observed germination was excessively high (P-value <0.001) for both models and at the 99% confidence level the larger model may not be any better than the model based just on Rainy Days ($\chi^2 = 16.60$; DF = 5; P-value = 0.012). Subpopulation was not a significant predictor in any model; which allows the data to be analysed as a single large set.

These analyses provide evidence that while a complex interplay of climatic variables influences germination, aggregating climatic variables as annual values (totals or averages) is too coarse to elucidate their effect on germination.
4.6.2 Mediterranean Climate

There were insufficient degrees of freedom (i.e. large enough sample) available for me to investigate differences between subpopulations in this analysis. However as sub-population had not been shown to be significant in either of the previous models above, it was again unlikely to be a significant predictor of germination.

Disregarding Subpopulation for this (and all subsequent) model(s) I performed stepwise logistical regression. I started the analysis with a model that had the four rainfall metrics (Rainfall, Rainy Days, Rain Intensity, and Cyclones) and Diurnal Temperature Range. From this model I removed the least significant predictors (i.e. lowest p-value) one at a time. This produced in the optimum model:

\[
\ln(\text{odds ratio}) = 28.0 - 0.01 \text{ Dry Season Rainfall} + 0.16 \text{ Dry Season Intensity} - 0.43 \text{ Wet Season Intensity} - 2.06 \text{ Wet Season Average Monthly Diurnal Temperature Range.}
\]

This model is significantly better than the null effect model (\(\chi^2 = 126.267; \text{ DF} = 4; \text{ P-value} < 0.001\)), the values predicted are a good fit with the values generated for the saturated statistical model with all predictors included (\(\chi^2 = 8.981; \text{ DF} = 6; \text{ P-value} = 0.175\)). This model provides a reasonable prediction of germination in the field, providing evidence that the bimodal climate of SWWA influences germination of \(V. \text{ staminosa}\).

4.6.3 The Traditional Four Seasons

Again, the problem of insufficient degrees of freedom meant that I could not analyse the model with four rainfall metrics (Rainfall, Rainy Days, Rain Intensity, and Cyclones) and Diurnal Temperature Range with twice as many (i.e. four) seasons. To determine if I could detect any relationships between climatic variables and germination under the Four Seasons climate I initially investigated the influence of rainfall and number of rain days. These metrics show significant inter-year variability for their annual values, had the greatest significance in my analyses of the annual metrics, and are suggested as being the most important in the literature (Cowling et al. 2005; Fay 2009). All seasons were significant when I logistically modelled both Rainfall and Rainy Days in isolation. By combining all the data for both these metrics and performing a standard stepwise logistical regression I generated the germination model:
Impact of climatic factors on germination of the rare shrub *V. staminosa*

\[
\text{Ln(oDDS ratio)} = -5.01 - 0.02 \text{ Summer Rainfall} - 0.01 \text{ Winter Rainfall} \\
+ 0.02 \text{ Spring Rainfall} + 0.19 \text{ Summer Rainy Days} + 0.11 \text{ Autumn Rainy Days} + 0.20 \text{ Winter Rainy Days}.
\]

This model is significantly better than the null effect model \((\chi^2 = 130.8; \text{ DF} = 6, \text{ P-value} < 0.001)\) and does not deviate significantly from values predicted by the saturated model \((\chi^2 = 4.349; \text{ DF} = 4; \text{ P-value} = 0.361)\). This model will provide a reasonable prediction of germination in the field.

Having found the most significant season predictors for Rainfall and Rainy Days, I attempted to add Intensity and Cyclones to the model. Again the available degrees of freedom were less than the requirements of this model. I chose not to model Summer Cyclones, which were not significant in the optimum germination model for the Mediterranean climate nor when compared to just Autumn Cyclones under the Four Seasons climate. With Autumn Cyclones included, I created four models each of which had the Rainfall Intensity of a different season left out. I then performed another stepwise regression on the most significant of the four models assessed in terms of the P-values of the predictors, difference from the Null Model as measured by the P-value of the test for all slopes being zero, and the P-value of the Deviance. This produced the following model for germination in the Four Seasons Climate:

\[
\text{Ln(oDDS ratio)} = -0.20 - 0.01 \text{ Summer Rainfall} + 0.01 \text{ Winter Rainfall} \\
+ 0.01 \text{ Spring Rainfall} + 0.07 \text{ Autumn Rainy Days} + 0.54 \text{ Autumn Cyclones} - 0.53 \text{ Winter Intensity}.
\]

Significantly better than the null effect model \((\chi^2 = 132.2; \text{ DF} = 6, \text{ P-value} < 0.001)\) and the values predicted from this model do not deviate significantly from the saturated model \((\chi^2 = 3.014; \text{ DF} = 4; \text{ P-value} = 0.555)\). Hence this model also provides a reasonable prediction of germination in the field.

To determine if this model could be further enhanced I added the diurnal temperature range data and again undertook stepwise logistical regression to produce the optimum germination model:

\[
\text{Ln(oDDS ratio)} = -25.9 + 0.03 \text{ Summer Rainfall} + 0.30 \text{ Autumn Rainy Days} \\
+ 0.87 \text{ Autumn Cyclones} + 1.19 \text{ Autumn Avg Monthly Diurnal Temp Range} - 0.88 \text{ Winter Avg Monthly Diurnal Temp Range} \\
+ 0.93 \text{ Spring Avg Monthly Diurnal Temp Range}.
\]
Again this model is significantly better than the null effect model ($\chi^2 = 134.0$; DF = 6, P-value <0.001) and predicted values do not deviate significantly from saturated statistical model ($\chi^2 = 1.208$; DF = 4; P-value = 0.877). This model also provides a reasonable prediction of field germination.

### 4.6.4 Six Noongar Seasons

The available degrees of freedom were taxed even further by the inclusion of the additional two seasons, which introduced an additional eight predictors, required under the six Noongar Seasons. To counter this problem I separately stepwise modelled the impact of the number of Rainy Days and the amount of the Rainfall in each season and then combing these models I again progressively removed the least significant terms. The germination model of Rainfall and Rainy Day predictors produced by this process was not a good fit to the observed data (H0: Model is a good fit to data; $\chi^2 = 12.13$; DF = 5; P-value = 0.033). I then added the two seasons with Cyclones and this produced the germination model:

$$\text{Ln(odds ratio)} = -4.53 - 0.49 \text{Bunurua Rainy Days} + 0.87 \text{Bunurua Cyclones} + 0.37 \text{Djeran Rainy Days} - 0.02 \text{Makuru Rainfall} + 0.10 \text{Makuru Rainy Days} + 0.15 \text{Djilba Rainy Days}.$$

This model is significantly better than the null effect model ($\chi^2 = 133.0$; DF = 6; P-value <0.001) and is a good fit to values generated for the saturated model with all predictors included ($\chi^2 = 2.244$; DF = 4; P-value = 0.691). As such this model will provide a reasonable prediction of germination in the field under the six Noongar Seasons. With the limited degrees of freedom available this is the optimum model I am able to produce for the Noongar Seasons. With the existing data set Minitab 15.0 could not resolve more complex models that included predictors for the rain intensity and diurnal temperature range.

### 4.6.5 Ranking the Season Models

Applying Burnham and Anderson’s (2002) approach to Akaike’s Information Criterion (1973; cited in Burnham and Anderson 2002) to ranking the logistical germination models reported above (Sections 4.6.2-4.6.4) generated the values in Table O.

This analysis provides evidence that the final model for germination under the Four Seasons (Section 4.6.3), which includes terms for amount of rainfall; number of rainy days; cyclone/tropical lows; and diurnal temperature variation,
is the ‘top model’ and the model for the six Noongar Seasons is next best. At the 95% confidence level the model for the Mediterranean climate has only marginal significance.

**Table N**: Ranking of logistical models for germination based on Burnham and Anderson’s (2002) approach to calculating AIC values (Larger the probability the better the model).

<table>
<thead>
<tr>
<th>Germination Model</th>
<th>AIC</th>
<th>AIC Difference</th>
<th>Model Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mediterranean Climate</td>
<td>569.92</td>
<td>3.774</td>
<td>0.060</td>
</tr>
<tr>
<td>Four Seasons – Rainfall &amp; Rainy Days</td>
<td>569.29</td>
<td>3.142</td>
<td>0.088</td>
</tr>
<tr>
<td>Four Seasons – with Intensity added</td>
<td>567.95</td>
<td>1.806</td>
<td>0.172</td>
</tr>
<tr>
<td>Four Seasons – with Diurnal Range</td>
<td>566.14</td>
<td>0.000</td>
<td>0.424</td>
</tr>
<tr>
<td>Six Noongar Seasons</td>
<td>567.18</td>
<td>1.036</td>
<td>0.252</td>
</tr>
</tbody>
</table>
Chapter 5: Discussion

5.1 Longevity of Seeds in Soil Seed Bank

With approximately 10% of the originally viable *V. staminosa* seeds germinating after being buried for seven years, my study is yet another demonstration of the fact that in Australia pericarp clad hard seeds can persist in the soil seed bank for extended periods of time (Tieu and Egerton-Warburton 2000; Fenner and Thompson 2005; Merritt et al. 2007). For the morphologically similar *Verticordia fimbrilepis* Yates and Ladd (2005) observed a strong decline in the viability of seeds that had been buried for 30 months and hypothesised that viable seed would remain in the soil seed bank for less than ten years. The results reported in Section 4.3 of this study suggest that *V. staminosa* seeds may be able to persist in the soil seed bank for longer than ten years, but a more structured long-term study is required to quantify my observations. Being unsure of the persistence of the soil seed bank, the population viability analysis for *V. staminosa* of Yates et al. (2007) adopted a highly conservative approach by assuming that no soil seed bank was carried over from year to year. My finding of a highly persistent seed bank would further enhance the stability of the Wongan Hills *V. staminosa* meta-population, supporting the hypothesis of Yates et al. (2007).

My analysis of rainfall over the time that these seeds were buried demonstrated that there were numerous years in which viable seeds could have become imbibed and germinated. The persistence of approximately 10% of the originally viable seeds for seven years after burial is consistent with previous studies of dormancy mechanisms and soil seed banks for hard seeded Australian species (Leishman & Westoby 1998; Fenner and Thompson 2005). It is likely that a combination of physical dormancy imposed by the pericarp and physiological dormancy, whereby imbibed seeds that have not germinated desiccate as the weather become drier and warmer late in the year and return to a state of secondary dormancy, contributes to longevity of *V. staminosa* seeds in the soil (Fenner and Thompson 2005; Merritt et al. 2007; Cousens et al. 2010).

5.2 Impact of Smoke Water and Weathering on Germination

Starting with Dixon et al. (1995) a great deal of prominence has been given to the role of smoke and solutions of smoke products (i.e. smoke water) in breaking the dormancy of Australian native species, particularly species of the SWBP.
However as I detailed in Section 2.3.2, in recent years there has been a shift in understanding to the point where smoke products in the soil are viewed as one of the many triggers that promote germination of an imbibed seed (Tieu and Egerton-Warburton 2000; Pickup et al. 2003; Merritt et al. 2007). As previously mentioned (Section 2.3.1), several authors contend that temperature is the primary factor, possibly the only factor, that alleviates seed dormancy (Tieu and Egerton-Warburton 2000; Pickup et al. 2003; Fenner and Thomson 2005; Merritt et al. 2007).

As smoke pre-treatment had been shown to increase germination rates in several species of *Verticordia* (E.A. George 2002; Yates and Ladd 2004), my soaking of *V. staminosa* seeds in Kings Park smoke water for one hour was very much related to using smoke to ‘break the dormancy’ of *V. staminosa* seeds. The fact that I found no evidence that smoke treatment alleviates dormancy (Section 4.4) appears consistent with the growing view that smoke does not alleviate dormancy in Australian seeds with a pericarp. Upon reflection Yates and Ladd (2004) applied their smoke water treatment directly to the soil seed bank. This could have facilitated germination of seeds that had their dormancy alleviated and were already imbibed. Additionally, up to a third of seeds in the soil seed bank will germinate, even without the presence of aqueous smoke products (Pickup et al. 2003; Nield et al. 2009).

While not increasing the number of seeds that germinate overall, repeated wetting and drying (hydration) cycles have been demonstrated to increase the rate of seedling emergence (Lush et al. 1984; Pickup et al. 2003; Fenner and Thomson 2005). However, I found no evidence of this effect in my experiment (Section 4.4).

I did observe that the ‘aged’ seeds recovered from the cracks and soil aprons on average germinated almost 11 days faster than seeds from the contemporary soil seed bank (Section 4.5). This increased rate of germination could be explained by greater weathering of the seed coat allowing moisture to reach the seed more rapidly, which results in faster imbibition and germination of the non-dormant seed (Lush et al. 1984; Martyn et al. 2009; Cousens et al. 2010)

### 5.3 Impact of Climatic Variables on Germination

In Section 4.6 I detail a number of models to describe the impact of climatic variables on germination within seasons and for different seasons. All the
models are valid for the metrics and seasons to which they relate and all provide insight into how a complex interplay of climatic factors may influence germination of *V. staminosa* seedlings. Using techniques of Stepwise Regression, Sequential Addition, Forward Selection, and Backward Elimination to develop a suite of models that contain different ‘significant’ predictors is a common approach in hypothesis forming logistical analyses (Tabachnick and Fidell 1996; Ramesy and Schafer 2002).

Ordering of the models using Burnham and Anderson’s (2002) approach to Akaike’s Information Criterion (1973; cited in Burnham and Anderson’s 2002) provides evidence that a combination of the amount of rainfall, the number of rainy days, the impact of tropical cyclones/lows, and diurnal temperature variation modelled in the traditional Four Seasons climate best describes germination of *V. staminosa* seedlings (P-value = 0.424). The model for the Six Noongar Seasons was the next best (P-value = 0.252), even though limitations caused by the relatively small size prevented the significance of terms for rainfall intensity and diurnal variation being assessed. Interestingly the optimum Mediterranean Climate model for germination of *V. staminosa* seedlings, which was developed utilising all the climate variables in a single analysis, has only marginal significance (P-value = 0.060).

Considering a suite of models also goes someway to addressing the issue that predictors that were considered ‘not significant’ and removed from a preliminary model may well become significant when included with another predictor added latter in the analysis (Ramesy and Schafer 2002). Also, given the limitations of the sample size and the high leverage (i.e. influence of outliers) generated by modelling extreme events, such as cyclones or extremely wet and dry years, care has to be taken interpreting the models and the predictions about germination that they suggest. The two best models for the traditional Four Seasons and the six Noongar Seasons (Sections 4.6.3 and 4.6.4) provide strong evidence that:

- The passage of a tropical cyclone or tropical low across the region creating a pulse of germination.
- The more rainy days (>1mm of rainfall) that occur in late autumn the greater the amount of germination that will occur.
- Surprisingly, higher winter rainfall reduces germination.
Impact of climatic factors on germination of the rare shrub *V. staminosa*

In relation to the diurnal temperature range, a metric that could not be incorporated in the Noongar Seasons modelling, the model for the traditional Four Seasons provides strong evidence that:

- The greater the diurnal temperature range in autumn (i.e. hotter the days and/or cooler the nights) the greater the germination.
- There is less germination in winter with higher diurnal temperature ranges, which would also equate to higher average daily temperatures.

The two models contradict each other in relation to the effect of summer rainfall. The Four Season model suggests it may result in a very slight increase in germination while the Noongar Season model suggests a very slight decrease. The magnitude of the predicted change in germination either way is marginal, but this provides a good example of why it often pays to consider a suite of logistical models, rather than basing firm predictions about biological systems on a single theoretical model.

The rainfall and diurnal temperature predictors of the best Four Seasons model are consistent with modelling of Nicholls et al. (2001) from the Australian Bureau of Meteorology Research Centre, who developed ‘skilful’ models for wheat production in SWWA that utilised monthly rainfall values and diurnal temperature ranges as predictors. Further, both the Four Seasons model and the Noongar Seasons models provide strong evidence in support of Cowling’s et al. (2005) hypotheses about the role of rainfall variability. My study provides strong evidence that in addition to the amount of rainfall, the seasonality of rainfall, the number of rainfall events (days), and the passage of tropical cyclones/lows can significantly influence the structure of vegetation in SWWA. At a finer scale, Merritt et al. (2007) postulates germination of non-dormant seeds was enhanced by warm stratification in moist soil in April and May. They attributed this effect to early rains moistening the soil while mean daily temperature were ≥15°C and the mean diurnal temperature range was >5°C. This observation fits with predictions of both models that a higher diurnal temperature range and/or rain in autumn increase germination. The impact of higher temperatures during this period can be attributed to the role of temperature in alleviating dormancy (Fenner and Thomson 2005; Merritt et al. 2007; Counsens et al. 2010).

The prediction of both models that the passage of tropical cyclones/lows during autumn will generate a pulse of germination is consistent with Schwinning’s et al.
(2004) hypothesis that a combination of rare large recruitment events (pulses) and low continuous recruitment are important for maintaining populations of long-lived perennial plants growing in semiarid environments. Cyclone induced germination of dicotyledon plants has also been observed in the adjoining Murchison region and a pulse in the germination of *V. staminosa* seedlings was reported after the passage of two cyclones between February and March 1999 (Mott 1972; Mott 1973; Yates and Ladd 2004; Australian Bureau of Meteorology 2011).

The inclusion of germination data from years with extreme weather conditions, such as cyclones and anomalously wet or dry years, resulted in all models having reasonably high levels of leverage, that is the impact of single or a few outliers strongly influenced the values of coefficients and the significance of predictors (variables) of the models reported in Section 4.6. As a result caution needs to be applied in interpretation of the models and predictions arising from that interpretation (Ramesy and Schafer 2002). However, in modelling climate related phenomena it is only these rare extreme events that produce statistically significant variation in the systems being studied (England et al. 2006). After analysing climate data of 5-6 years duration England et al. (2006) stated “A much longer observational record is required to obtain detailed statistically significant patterns ... during wet and dry years over SWWA.” This demonstrates the immense value of the long term study of *V. staminosa* germination that I utilised to produce the modelling in this study.
Chapter 6: Conclusions and Recommendations

6.1 Conclusions

My investigation found no evidence of either smoke treatment or repeated wetting and drying of ripe fruit alleviating dormancy or increasing the rate of germination of *V. staminosa* seeds in the soil seed bank. However, my study demonstrates that long term in-situ weathering of soil stored seed significantly increases the rate at which a non-dormant seed will become imbibed and germinate in response to cues or triggers in its microenvironment.

The germination models I developed in this study challenge the established view that the amount of annual or ‘wet season’ rainfall is the significant driver of germination in the Southwest Botanical Province. These models demonstrate that instead a complex interplay of rainfall characteristics, such as amount and timing of rainfall and number of rainy (≥2mm) days, temperature variables, especially diurnal variation, and extreme climatic events (cyclones/intense tropical lows) provide germination triggers for of *V. staminosa*.

In terms of the research questions I posed at the commencement of my study, I found strong evidence to reject all three null hypotheses in favour of the alternate hypotheses that:

- The amount and timing of rainfall does influence germination of *V. staminosa* seedlings.
- Air temperature, in particular the diurnal temperature range, in combination with the amount of rainfall, the number of rainy days; and/or the rain intensity (amount/event) influences germination of *V. staminosa* seedlings.
- The age of fruit in the soil seed bank influences germination of *V. staminosa* seedlings.

6.2 Recommendations for Future Research

A number of papers published over the last decade have identified shortcomings in the experimental design and/or challenged the conclusions of earlier and concurrent research (Hughes 2003; Moles and Westoby 2004; Merritt et al. 2007; Cousens et al. 2010). Similar to Cousens’ et al. (2010) research into the role of the pericarp in dormancy and imbibition of the seed, my research has raised as many questions as it has (possibly) answered. There is clearly a need for better
designed experiments with larger sample sizes that investigate phenomena of interest at a finer spatial and temporal scale for longer periods (e.g. several years at least) for a range of rare and common conjoiner species across the SWBP. Specifically there need to be additional research into:

- Dormancy mechanisms and germination triggers for fresh (current season) *Verticordia* fruit compared to fruit in the soil seed bank.
- The role of the pericarp (if any) in imposing physical and/or physiological dormancy and controlling imbibition and desiccation of *Verticordia* seeds.
- Long term (7+ years) trails of soil seed bank persistence.
- Short (months and season) and long term (7+ years) study of the viability and germinability of soil stored fruits of known age.
- Seasonal scale investigation of the impact of weather on seedling germination and survival within and between seasons for a minimum of three years.
- Establishment and maintenance of long term monitoring of seedling germination and survival, as has been occurring with the Wongan Hills *V. staminosa* meta-population since 1999.
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## Appendices

### A. Exploratory Analyses: Ex-situ Germination Experiments

#### A1 Seed Viability of the Soil Seed Bank

![Histogram and Box & Whisker Plot](image1)

**Figure A1.1:** Combined Histograms and the Box & Whisker Plot for pericarps found not contain a seed in the 3 ‘Cut Seed’ Trials.

![Histogram and Box & Whisker Plot](image2)

**Figure A1.2:** Combined Histograms and the Box-Whisker Plot for pericarps found to contain a seed in the 3 ‘Cut Seed’ Trials.

#### A2 Germination Response of Recovered Pericarp

![Histogram and Box & Whisker Plot](image3)

**Figure A2.1:** Combined histograms and Box & Whisker Plots for number of seedlings that emerged in replicates of recovered pericarps.
Impact of climatic factors on germination of the rare shrub *V. staminosa*

**Figure A2.2:** Combined histograms and Box & Whisker Plots for time taken for seedlings to emerge in replicates of recovered pericarps.

**Figure A2.3:** Combined histograms and Box & Whisker Plots for percentage of originally viable seeds that germinated in replicates of recovered pericarps.

### A3 Impact of Smoke and Weathering on Germination

**Figure A3.1:** Combined Histograms for number of seedlings to emerge for each germination treatment (Left) and the Log(x) transformed data of the same metric (Right)
Impact of climatic factors on germination of the rare shrub *V. staminosa*

**Figure A3.2:** Box & Whisker Plots for the number of seedlings that emerged for each germination treatment with raw data on the left and Log-transformed data is on the right.

**Figure A3.3:** Box & Whisker Plots for the number of seedlings with each Tray of replicates. Again raw data is shown on the left and Log-transformed data is on the right.

**Figure A3.4:** Combined Histograms of raw data (Left) and Log(x) transformed data of the average time taken for seedlings of each treatment to emerge within a Tray.
Figure A3.5: Box & Whisker Plots of average time taken for seedlings with each treatment to emerge within a Tray. Raw data on left and Log-transformed data on right.

Figure A3.6: Box & Whisker Plots of average time taken for seedlings to emerge within a Tray. Again the raw data is on the left and Log(x) transformed data is on the right.

Figure A3.7: Box & Whisker Plots for the proportion of viable seeds that produced seedlings with raw data is shown on the left and Log(x) transformed data is on the right.
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**B. Exploratory Analyses: Field Germination**

**B1  Seedling Germination in the Field**

**Figure B1.1** Combined Histograms and Box & Whisker Plot showing the between year variability in the proportion of quadrats in each subpopulation that contained seedlings.

**Figure B1.2** Combined Histograms and Box & Whisker Plots showing the between year variability in the total number of seedlings in each subpopulation.

**Figure B1.3:** Combined Histograms and Box & Whisker Plot showing the between year variability in the average number of seedlings per quadrat by subpopulation.
C. Exploratory Analyses: Seasons of SW Western Australia

C1  Annual Values

Figure C1.1: Histograms and Box & Whisker Plots showing between year variability in the Annual Rainfall (Top), the annual number of Rainy Days (more than 1mm of rain in 24 hours), and Annual Rainfall Intensity (Annual Rainfall averaged over the annual number of Rainy Days), for the 20 year period from 1991 to 2010.

Figure C1.2: Between year variability in Annual Average Monthly Solar Radiation 1991-2010.
Impact of climatic factors on germination of the rare shrub *V. staminosa*

**Figure C1.3**: Between year variability in Annual Average Monthly Temperature 1991-2010.

**Figure C1.4**: Between year variability in Annual Average Monthly Maximum Temperature for the 20 year period between 1991 and 2010.

**Figure C1.5**: Histogram and Box & Whisker Plot showing between year variability in the Annual Average Monthly Minimum Temperature from 1991 to 2010.

**Figure C1.6**: Between year variability in the Annual Average Monthly Diurnal Temperature Range for the period 1991 to 2010.
C2 Mediterranean (Dry/Wet Seasons) Values

Figure C2.1: Histograms and Box & Whisker Plot showing between year variability in the Dry Season (Nov-May) Rainfall and the Wet Season (Apr-Oct) Rainfall from 1991 to 2010.

Figure C2.2: Histograms and Box & Whisker Plot showing between year variability in the number of Rainy Days in the Dry Season and in the Wet Season from 1991 to 2010.
Impact of climatic factors on germination of the rare shrub *V. staminosa*

**Figure C2.3:** Histogram and Box & Whisker Plot showing between year variability in Rainfall Intensity in the Dry Season and in the Wet Season (measured as Average Rainfall per Rainy Day) for the 20 year period 1991-2010.

**Figure C2.4:** Histograms and Box & Whisker Plot showing between year variability in the Average Monthly Solar Radiation for the Dry Season and the Wet Season from 1991-2010.
Impact of climatic factors on germination of the rare shrub *V. staminosa*

**Figure C2.5:** Histograms and Box & Whisker Plot showing between year variability in the Average Monthly Temperature for the Dry Season and the Wet Season from 1991 to 2010.

**Figure C2.6:** Histograms and Box & Whisker Plot showing between year variability in the Average Monthly Maximum Temperature during the Dry Season and the Wet Season for the 20 year period from 1991 to 2010.
Impact of climatic factors on germination of the rare shrub *V. staminosa*

**Figure C2.7:** Between year variability in the Average Monthly Minimum Temperature for the Dry Season and the Wet Season in the period from 1991 to 2010.

**Figure C2.8:** Histograms and Box & Whisker Plot showing between year variability in the Average Monthly Diurnal Temperature Range for the Dry Season and the Wet Season in the 20 year period between 1991 and 2010.
C3 Four Seasons Values

Figure C3.1: Histograms and Box & Whisker plots showing between year variability in Rainfall for each of the 4 seasons for the 20 year period between 1991 and 2010. Summer season is from December to February, Autumn covers March to May, Winter is June to August, and Spring falls in the months of September to November.
Figure C3.2: Histograms and Box & Whisker Plot showing between year variability of the Number of Rainy Days in each of the 4 seasons during the period 1991 to 2010.
Impact of climatic factors on germination of the rare shrub *V. staminosa*

Figure C3.3: Histogram and Box & Whisker Plot showing between year variability in Rainfall Intensity (measured as Average Rainfall per Rainy Day) across the 4 season for the 20 year period from 1991 to 2010.
Figure C3.4: Histograms and Box & Whisker Plot showing between year variability in the Average Monthly Solar Radiation for the 4 seasons over the period 1991-2010.
Figure C2.5: Histograms and Box & Whisker Plot showing between year variability in the Average Monthly Temperature for the 4 season in the 20 year period 1991 to 2010.
Figure C2.6: Histograms and Box & Whisker Plot showing between year variability in the Average Monthly Maximum Temperature during the 4 seasons between 1991 and 2010.
Figure C2.7: Between year variability in the Average Monthly Minimum Temperature during the 4 seasons between Summer and Spring in the years 1991 to 2010.
Figure C2.8: Histograms and Box & Whisker Plot showing between year variability in the Average Monthly Diurnal Temperature Range for each of the 4 seasons from 1991 to 2010.
Figure C4.1: Histograms and Box & Whisker Plot showing between year variability (1991-2010) in Rainfall for the six Noongar seasons of the SWBP.
Figure C4.2: Histograms and Box & Whisker Plot showing between year variability in the number of Rainy Days in each of the Noongar seasons in the period 1991 to 2010.
Figure C4.3: Histograms and Box & Whisker Plot of between year variability (1991-2010) in Rainfall Intensity (i.e. Average Rainfall per Rainy Day) for the six Noongar seasons.
Figure C4.4: Histograms and Box & Whisker Plot showing between year (1991-2010) variability in the Average Monthly Solar Radiation for the six Noongar seasons.
Impact of climatic factors on germination of the rare shrub *V. staminosa*

**Figure C4.5:** Histograms and Box & Whisker Plot showing between year variability (1991 to 2010) in the Average Monthly Temperature for each of the six Noongar seasons.
Figure C4.6: Histograms and Box & Whisker Plot showing between year (1991-2010) variability in the Average Monthly Maximum Temperature for the six Noongar seasons.
Impact of climatic factors on germination of the rare shrub V. staminosa

Figure C4.7: Between year variability in the Average Monthly Minimum Temperature for the Dry Season and the Wet Season in the period from 1991 to 2010.
Impact of climatic factors on germination of the rare shrub *V. staminosa*

**Figure C4.8:** Histograms and Box & Whisker Plot showing between year variability in the Average Monthly Diurnal Temperature Range for each of the six Noongar seasons.
**Impact of climatic factors on germination of the rare shrub *V. staminosa***

### D. Outcomes of Least Squares Regression Analyses of Correlation between Annual Climate Metrics

The Pearson’s Coefficient of Correlation ($R^2$) for each pair of climate metrics is reported on the lower left and the significance of each $R^2$ value is reported on the upper right. Significant correlations are shown in red.

|-----------------|-------------------|-----------------------|-------------------------------|---------------------------|--------------------------------|--------------------------------|---------------------------------|
| **Annual Rainfall** | F = 29.06  
      P-value < 0.001 | F = 7.046  
      P-value = 0.016 | F = 1.506  
      P-value = 0.235 | F = 8.262  
      P-value = 0.010 | F = 1.304  
      P-value = 0.268 | F = 14.07  
      P-value = 0.001 | F = 5.691  
      P-value = 0.029 |
| **Annual Rainy Days** | 61.8% | F = 0.181  
      P-value = 0.676 | F = 1.402  
      P-value = 0.252 | F = 10.25  
      P-value = 0.005 | F = 2.349  
      P-value = 0.143 | F = 23.00  
      P-value < 0.001 | F = 7.210  
      P-value = 0.015 |
| **Annual Rain Intensity** | 28.1% | 1.0% | F = 0.269  
      P-value = 0.610 | F = 0.230  
      P-value = 0.638 | F = 0.102  
      P-value = 0.753 | F = 0.049  
      P-value = 0.827 | F = 0.074  
      P-value = 0.789 |
| **Annual Avg. Monthly Solar Rad.** | 7.7% | 7.2% | 14.7% | F = 44.87  
      P-value < 0.001 | F = 14.98  
      P-value = 0.001 | F = 1.828  
      P-value = 0.193 | F = 14.38  
      P-value = 0.001 |
| **Annual Avg. Monthly Temp.** | 31.5% | 36.3% | 1.2% | 71.4% | F = 0.565  
      P-value = 0.462 | F = 25.49  
      P-value < 0.001 | F = 29.94  
      P-value < 0.001 |
| **Annual Avg. Monthly Max. Temp.** | 6.7% | 11.5% | 0.6% | 45.4% | 3.0% | F = 5.943  
      P-value = 0.025 | F = 0.374  
      P-value = 0.548 |
| **Annual Avg. Monthly Min. Temp.** | 43.9% | 56.1% | 0.3% | 9.2% | 58.6% | 24.8% | F = 10.17  
      P-value = 0.005 |
| **Annual Avg. Monthly Diurnal Range** | 24.0% | 28.6% | 0.4% | 44.4% | 62.4% | 2.0% | 36.1% |
### Correlation Analyses for Noongar Seasons Temperature Metrics

#### Biruk (Dec-Jan)

<table>
<thead>
<tr>
<th></th>
<th>Average Monthly Diurnal Range</th>
<th>Avg Monthly Max Temp</th>
<th>Avg Monthly Solar Radiation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Avg Monthly Diurnal Range</td>
<td></td>
<td>F = 24.26 P-value&lt;0.001</td>
<td>F = 19.89 P-value&lt;0.001</td>
</tr>
<tr>
<td>Avg Monthly Max Temp</td>
<td>R² = 0.574</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Avg Monthly Solar Radiation</td>
<td>R² = 0.525</td>
<td>R² = 0.470</td>
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</tbody>
</table>

#### Bunurua (Feb-March)

<table>
<thead>
<tr>
<th></th>
<th>Average Monthly Diurnal Range</th>
<th>Avg Monthly Max Temp</th>
<th>Avg Monthly Solar Radiation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Avg Monthly Diurnal Range</td>
<td></td>
<td>F = 29.38 P-value&lt;0.001</td>
<td>F = 13.59 P-value=0.002</td>
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<tr>
<td>Avg Monthly Max Temp</td>
<td>R² = 0.620</td>
<td></td>
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<tr>
<td>Avg Monthly Solar Radiation</td>
<td>R² = 0.430</td>
<td>R² = 0.051</td>
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</table>

#### Djeran (April-May)

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<th>Average Monthly Diurnal Range</th>
<th>Avg Monthly Max Temp</th>
<th>Avg Monthly Solar Radiation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Avg Monthly Diurnal Range</td>
<td></td>
<td>F = 7.023 P-value=0.016</td>
<td>F = 7.016 P-value=0.015</td>
</tr>
<tr>
<td>Avg Monthly Max Temp</td>
<td>R² = 0.281</td>
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</tr>
<tr>
<td>Avg Monthly Solar Radiation</td>
<td>R² = 0.283</td>
<td>R² = 0.008</td>
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</table>

#### Makuru (June–July)

<table>
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<th>Average Monthly Diurnal Range</th>
<th>Avg Monthly Max Temp</th>
<th>Avg Monthly Solar Radiation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Avg Monthly Diurnal Range</td>
<td></td>
<td>F = 10.39 P-value=0.005</td>
<td>F = 10.33 P-value=0.005</td>
</tr>
<tr>
<td>Avg Monthly Max Temp</td>
<td>R² = 0.366</td>
<td></td>
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<tr>
<td>Avg Monthly Solar Radiation</td>
<td>R² = 0.365</td>
<td>R² = 0.121</td>
<td></td>
</tr>
</tbody>
</table>
### Impact of climatic factors on germination of the rare shrub *V. staminosa*

#### Djilba (Aug-Sept)

<table>
<thead>
<tr>
<th></th>
<th>Average Monthly Diurnal Range</th>
<th>Avg Monthly Maximum Temp</th>
<th>Avg Monthly Solar Radiation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Avg Monthly Diurnal Range</td>
<td></td>
<td>F = 20.05</td>
<td>F = 12.57</td>
</tr>
<tr>
<td>Avg Monthly Max Temp</td>
<td>R² = 0.52.7%</td>
<td>P-value&lt;0.001</td>
<td>P-value&lt;0.001</td>
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<tr>
<td>Avg Monthly Solar Radiation</td>
<td>R² = 0.41.1%</td>
<td>R² = 0.48.4%</td>
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</tbody>
</table>

#### Kambarang (Oct-Nov)

<table>
<thead>
<tr>
<th></th>
<th>Average Monthly Diurnal Range</th>
<th>Avg Monthly Maximum Temp</th>
<th>Avg Monthly Solar Radiation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Avg Monthly Diurnal Range</td>
<td></td>
<td>F = 26.82</td>
<td>F = 6.311</td>
</tr>
<tr>
<td>Avg Monthly Max Temp</td>
<td>R² = 0.59.8%</td>
<td>P-value&lt;0.001</td>
<td>P-value=0.022</td>
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<tr>
<td>Avg Monthly Solar Radiation</td>
<td>R² = 0.26.0%</td>
<td>R² = 0.21.2%</td>
<td></td>
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