# Regrowth and recruitment of the rare shrub *Logania saxatilis* in response to fire

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Cover images (from left to right, top to bottom): *Logania saxatilis* in bud at Telowie Conservation Park; prescribed burn at Mount Remarkable in 2011; flower of *L. saxatilis*; study site at Telowie Gorge Conservation Park; study site at Mount Remarkable

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## *Declaration*

I, Ute Susanne Grehn, certify that this work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

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# *Thesis summary*

This project investigated regrowth and recruitment response of the rare shrub *Logania saxatilis* (Rock Logania) after exposure to fire. Field monitoring took place in two reserves in the Southern Flinders Ranges, South Australia: Mount Remarkable National Park (Mount Remarkable) and Telowie Gorge Conservation Park (Telowie). The two sites differed in several aspects including vegetation and fire history. Telowie had been subject to a prescribed burn approximately 18 months earlier, while a fire at Mount Remarkable was planned for the near future which offered the opportunity for both pre- and post-burn assessment. Abundance, height, vigour and leaf size of regrowth were recorded on three burnt and five unburnt sites at each reserve. Strong post-fire regrowth of *L. saxatilis* was observed on all burnt sites, while unburnt sites had less or no new growth. At Mount Remarkable, analysis by ordination of individual morphology data clearly indicated the presence of regrowth from resprouting adults and seedlings. At Telowie, on the other hand, a fairly uniform seedling population was found. This regeneration behaviour of *L. saxatilis* is consistent with a facultative resprouter. Over the two-year monitoring period, growth and mortality led to significant changes in the populations, as confirmed by ANOVA. Resprouts rapidly reached height maturity, while seedlings grew more slowly. Summer drought appeared to be the main trigger of mortality in all seedling populations. Analyses by regression and by ANOVA showed that survival was also density dependent, i.e. reduced by proximity to other seedlings and to adults. First flowering of seedlings was observed at Telowie three years after fire. The effect of fire-related changes on seed germination was researched through *in vitro* germination tests, by exposing seed to fully crossed treatment combinations with heat, smoke-water, potassium nitrate and cold stratification. Incubation took place with or without light. Counts of germinating seed at one, two and eight weeks after start of incubation were analysed with five-factor ANOVA (JMP IN 4). While several effects were interactive, of single treatments the application of smoke-water had the strongest positive effect on germination rates, being equal in effect to the combination of heat and nitrate. Light and nitrate without heat also had a positive effect, while heat without nitrate and cold stratification did not; application of all treatments led to full germination.

This research concludes that fire, and to a lesser degree other disturbances, promote germination and establishment of *L. saxatilis*. Fire, for example through lightning strikes, is a natural factor in shaping at least some of the vegetation in the Southern Flinders Ranges and evolutionary adaptation to fire occurrence can be expected. Altered fire regimes, ranging from fire exclusion to frequent burning, form a potential threat to the species. Fire exclusion, especially in absence of other disturbances, may lead to senescence and gradual decline of some populations, while very high fire frequency may deplete the seed bank of species responding like *L. saxatilis*, and threaten population recovery, particularly when adults are lost and moisture availability is low.

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# 1 Introduction

## 1.1 Project Background

Fire is a natural occurrence in Mediterranean type vegetation, as lightning strikes on flammable plants during dry and hot summers render occasional fire inevitable (Whelan 1995). Plants and animals have evolved with intermittent exposure to wildfires and some thrive in the post-fire environment, while others temporarily decline in numbers, to eventually re-establish through migration from adjacent, unburnt areas at various times after fire (Whelan *et al.* 2002). These effects were well known to Australia's indigenous people, who developed a system of landscape management using fire (Morton *et al.* 2011). This system was disrupted by European settlement and much native vegetation was removed by pastoral use and particularly by agriculture (Natural Resources Management Board 2009). In many reserves of remnant vegetation, fires were excluded and suppressed especially during much of the 20th century (Pyke *et al.* 2010). In more recent times, the important ecological role of fire in maintaining habitat diversity in this environment has been recognised (Gill 1981). In addition to these ecological insights, there are rising public and administrative concerns that an absence of fire in nature reserves may lead to an accumulation of easily flammable fuel through vegetation growth, resulting in uncontrollable summer wildfires. It is feared that such fires may travel rapidly from reserves into adjacent private land as well as into townships and threaten human lives and assets (Bradstock *et al.* 1998).

**Fig 1-1 Prescribed burn site at Mount Remarkable during aerial ignition from helicopter, March 2011**

These concerns were much driven by the 2009 Black Saturday Bushfires in Victoria (Stuart Beinke, Regional Fire Management Officer for the Northern & Yorke Region South Australia, pers. comm.) which led to the loss of 173 lives and enormous destruction of property: the 2009 Victorian Bushfires Royal Commission, established nine days after the fires on 16 February 2009, had the purpose of investigating the “causes and responses to the bushfires” (2009 Victorian Bushfires Royal Commission 2010). The Commission delivered its Final Report on 31 July 2010, which included many recommendations aimed at preventing the reoccurrence of such an emergency. One of these was the development of a long term program of prescribed burning with a target of burning 5 % of public lands annually (2009 Victorian Bushfires Royal Commission 2010).

As South Australia has also adopted this recommendation, reserve managers are now expected to identify and burn strategically important areas within reserves to meet this target (Department for Environment, Water and Natural Resources DEWNR). However, this recommendation highlights the potential conflict between two key purposes of reserves under the National Parks and Wildlife Act (1972) and the South Australian Wilderness Protection Act 1992, which are the conservation of wildlife (including native flora) in a natural environment on the one side, and the “management for public benefit and enjoyment” including “the prevention and suppression of bush fires” on the other (National Parks and Wildlife Act 1972).

**Fig 1-2 Prescribed burn site at Telowie Gorge Conservation Park on right side of track approximately 18 months after the fire.**

Presumably in appreciation of this conflict, the approval process for prescribed burning in South Australia requires investigation into the effect of fire on all known native vertebrate animals and plants in the proposed burn zones. Particular attention is directed towards species with a conservation rating, adding urgency to the need to improve knowledge of fire responses of rare and threatened species.

One of the areas affected by an extension of the prescribed burning program is the Southern Flinders Ranges in South Australia (see Fig 1-1 & Fig 1-2). Currently, very little is known about the biology of species in the Southern Flinders (Natural Resources Management Board 2009) and about appropriate fire regimes to maintain biodiversity in this fragmented landscape, with particular view towards its rare and threatened species. One such plant is the Rock Logania (*Logania saxatilis*), a shrub restricted to the Mount Lofty, Flinders and Olary Ranges of South Australia. Given its limited distribution and rare status, management of reserves towards retaining this species is important. However, knowledge about the biology and ecology of this species is very poor; it is uncertain what effect fire may have on its populations (Department for Environment and Heritage 2010).

## *1.2 Thesis outline and research aims*

The purpose of this project was to determine the role fire, in particular prescribed burning, has in the recruitment and persistence of *L. saxatilis* populations in the Southern Flinders Ranges. A combination of field- and laboratory-based investigations was chosen:

1. A field study monitoring post-fire recovery of the species in two reserves with different fire histories, aspects and vegetation communities
2. A seed germination test under laboratory conditions to differentiate between the effects of disturbance with and without fire.

# *2 Background to research themes*

## *2.1 Effect of disturbances on plants with particular focus on fire*

Fire meets the definition of disturbance, being a "relatively discrete event in time that removes organisms and opens up space which can be colonised by individuals of the same or different species" (Begon *et al.* 1990). Other disturbances in rocky elevated environments such as the Southern Flinders Ranges can be for example rock or tree fall, erosion, severe storms, drought or plant disease, and animal or human activity.

Many forms of disturbance disrupt the soil surface and its cover, be it litter or plants, or reduce the tree canopy above, triggering changes in growth conditions for plants (Fig 2-1). Light influx may increase, and soil temperatures fluctuate in response to the daytime patterns of light and shade moving across the ground (Vincent and Roberts 1977). Bacterial activity involved in the decomposition of organic matter often leads to soil nitrification and improved nitrate availability (Sharrow and Wright 1977). These processes can enhance growth of existing plants and release dormancy of some soil stored seed, resulting in emergence of new plants (Goudey *et al.* 1988).

In comparison to other disturbances, fire has some additional, unique effects on vegetation, both destructive and regenerative. Initially, fire is often catastrophic for many individual plants and animals. However, the removal of large amounts of vegetation also represents an outstanding opportunity for new plant growth. The old plant matter, converted to ash, temporarily offers valuable mineral resources (Humphreys and Craig 1981) to support this growth. Therefore, many plants in environments subject to recurrent fire have evolved mechanisms to recognise and respond to fire specific changes in order to maximise growth and recruitment as soon as possible after fire (Fig 2-2). For example, heating of soil surfaces leads to the removal of physical dormancy of some hard-coated seeds. Smoke contains karrikins, which trigger germination of physiologically dormant seed of many plant species. In such plants, germination will follow exposure to smoke as soon as other essential conditions such as moisture and temperature are suitable for young seedlings. Adaptation to recruitment in the post-fire environment is strong in some species that seem to have completely dormant seed banks in the absence of fire (Campbell *et al.* 2012).

**Fig 2-1 Loss of canopy in a senescent *Eucalyptus cladocalyx* during prescribed burn at Wirrabara Forest, Southern Flinders Ranges**

Furthermore, the fire regime shapes vegetation through frequency, intensity, season and extent of fires. Fire frequency determines the time available for vegetation recovery between fires, be it by recruitment, vegetative regrowth, or migration of propagules into the burnt area after fire. Maturation and seed production must be possible at some time in the fire cycle for plant species to persist. According to Keith (1996) and Knox and Clarke (2006), a fire frequency which is too high exhausts resprouting capacity by diminishing bud banks and carbohydrate storage; recruited young obligate seeders are killed before maturity, and seed banks are depleted without recruitment success and recharge. Fire frequency which is too low can lead to a lack of recruitment in species dependent on fire for germination, and plants with short-lived seed banks may become extinct (Campbell *et al.* 2012). Therefore, either extreme of fire frequency potentially leads to species decline; this pattern meets the prediction of the Intermediate Disturbance Hypothesis (Fox and Connell 1979) which states that at an ideal intermittent frequency of disturbances, the diversity of species will be maximised. For fire responses, this would mean that tolerable fire frequencies for each species in the habitat would cluster around this “intermediate” figure. Fire intensity directly controls mortality rates of vegetation and the strength of trigger effects on germination, such as the removal of physical dormancy from seed through heat (Tieu *et al.* 2001). Low intensity fires improve survival chances of existing plants but may not allow for fire dependent recruitment to take place, for example due to inability of seedlings to succeed in presence of the established plants. High fire intensity leads to greater mortality of plants and their seeds but can trigger better germination of the remaining seeds of obligate seeders, and improve their chances of establishments because competition is reduced (Tyler 1995).

Fire season affects regeneration capacity through the availability of sufficient moisture or suitable temperatures during the initial stages of growth (Knox and Clarke 2006). Spring fires also interfere with flowering and seed production of many plants; furthermore, as summer progresses, desiccation causes mortality in young seedling emerged after the fire. On the other hand, cold and wet winters after autumn burning can also interfere with recruitment success (Knox and Clarke 2006).

**Fig 2-2 Regrowth from resprouts and seedlings after death of overstorey in an *Allocasuarina verticillata* woodland at a Telowie study site about 18 months after fire**

Prescribed burning is the “purposeful application of fire to the landscape” (Penman *et al.* 2011). It is applied through “patch burning” of relatively small, specifically targeted sites with built assets such as around tracks and buildings, or through “ecological“ burns covering much larger areas and aimed primarily at upholding a fire frequency suited to the vegetation type (Department for Environment, Water and Natural Resources 2012a). As pointed out above, regeneration after fire takes place through survival of species or their propagules on the burnt site itself, or through recolonisation from unburnt habitat in the periphery of the burn (Noble and Slatyer 1980). Recolonisation is the only option for species that cannot survive fire, or the changed conditions in their habitat after fire, such as many animals (Clarke 2008), but also certain plants. They may gradually reestablish from the margins of the burn, and some even require a certain age since fire for survival. However, modern fragmented landscapes leave individual reserves often isolated from each other and, therefore, restrict the movement of such species to and from unburnt habitat in response to fire, especially when large portions of a reserve are burnt (Kelly *et al.* 2012). It can be argued that the regeneration strategy through recolonisation is typically no longer available, and its absence can result in the risk of local extinction of plants or animals after fire.

## *2.2 Plant regrowth strategies*

After fire, vegetative growth, such as resprouting (Fig 2-3), and recruitment from seed (Fig 2-4) stored on site are the main pathways of regeneration of plants which do not depend on recolonisation from the unburnt periphery (Noble and Slatyer 1980). A robust regrowth response with either of these mechanisms would indicate the capacity of a plant population to survive at least an occasional fire event.

Conventionally, according to their strategy, species of plants are often classed as resprouters, obligate seeders or facultative resprouters, with certain attributes allocated particularly to the first two types. For example different growth rates and shapes, time to maturity, longevity and ability to compete have been suggested for either (Thomas and Davis 1989). Clearly, resprouting after canopy damage requires epicormic buds, which are located in trunks and branches of some species (Burrows 2013a), meristems in the leaf axils (Hodgkinson 1998), lignotubers, burls or roots with the capacity to establish suckers. Resprouters are aided by high root to shoot ratio, deep roots and nutrient stores in the root and crown, as stated by Thomas and Davis (1989), and by Pate *et al.* (1990b). They are also said to invest less resources in growth and reproduction under undisturbed conditions.

**Fig 2-3 Observation of basal resprouting in the study species *Logania saxatilis* at Mount Remarkable National Park in May 2011, 39 days after the prescribed burn**

Their great potential for vegetative regrowth even after the substantial damage inflicted by fire on the above ground parts of the plant results in quick recovery, and some or all of the same population as prior to disturbance persists. Resprouting offers the advantage of growth from an established root system, therefore usually avoiding the high mortality associated with seedlings. Obligate seeders have limited resilience to damage inflicted on individuals by fire although some temporary regrowth has been observed (Hodgkinson 1998). They are said to produce more seed, have better seedling growth and establishment rates, and reach reproductive maturity earlier than resprouters (Thomas and Davis 1989). Many factors affect the survival rates of seedlings and juveniles particularly in the early years of their life, with drought, frost, herbivory and disease being the most important reasons (Moles and Westoby 2004). Additionally, studies especially of tropical and temperate shrubs and trees have shown that the positioning of seedling in relation to each other and to adults also has an impact on survival (density dependent effects (Augspurger and Kelly 1984). Where population recovery relies on seedlings, success is dependent on benign conditions during the early stages of their lives (Whelan *et al.* 2002). If successful, this response form leads to a rejuvenation and even expansion of the population, while offering the possibility of a changed genetic composition that may offer better adaptation to current conditions. Facultative resprouters are an intermediate form between seeders and resprouters (Thomas and Davis 1989), where seedling growth is usually observed but resprouting is inconsistent. Their characteristics seem to be less clearly cut, although for example rapid resource acquisition and fast growth have been suggested (Vivian and Cary 2012). This response form also emphasizes the variability of regeneration capacity and pathways within a species. Possible factors are intraspecific differentiation into ecotypes (Benwell and McCorkell 2011), disturbance frequency (Croft *et al.* 2010), type (Benwell 2007) and intensity (Vivian *et al.* 2008) or habitat quality (Benwell 1998) such as soil type or nutrients (Benwell and McCorkell 2011) and the availability of moisture (Mendoza *et al.* 2009). Combinations of disturbances, especially when involving drought, can severely compromise regrowth capacity (Croft *et al.* 2010).

**Fig 2-4 Seedling emerged after fire**

Given the apparent multitude of factors contributing to the eventual regrowth response, it would seem prudent that investigations into the capacity and response mechanisms of plant populations after fire should include careful observations across more than one habitat and fire regime. This is particularly the case when assessing the potential of rare and endangered species to recover from prescribed burns and bushfires, which may affect much or all of their range within an isolated reserve.

## *2.3 The Rock Logania (*Logania saxatilis*)*

The family of the Loganiaceae includes about 500 species in 29 genera, mainly in the form of trees, shrubs, climbers and herbs, which occur predominantly in tropical and subtropical regions (Conn 2013). Economically relevant species are *Strychnos nux-vomica* L. which supplies strychnine and also *S. toxifera* Schomb. , the source of curare. The genus also contains a number of edible fruits such as for example *S. cocculoides,* the Corky-barked Monkey Orange. Seven genera with 25 species of Loganiaceae are indigenous to Australia. In South Australia, they are represented by the herbaceous *Mitrasacme* (one species) and *Phyllangium* (three), and ten *Logania* shrubs, together covering a wide range of habitats from coastal to far inland. Five species have a conservation rating under the National Parks and Wildlife Act (1972) as current in 2014: *Mitrasacme pilosa* Labill. *var. pilosa* (vulnerable), *Phyllangium distylis* (F.Muell.)Dunlop (rare), *P.sulcatum* Dunlop (vulnerable), *Logania insularis* J.M.Black (vulnerable), *Logania scabrella* B.J.Conn (rare) and *Logania saxatilis* G.Perry ex B.J.Conn (rare).

**Fig 2-5 *Logania saxatilis* (Rock Logania) on control site at Telowie Conservation Park**

*Logania saxatilis,* the Rock Logania (Fig 2-5), is previously referred to as *Logania* sp.B by Perry (1986) with reference to *Logania longifolia* R. Br. var. *brevifolia* Benth. (1868) and the now Western Australian *Logania vaginalis* (Black 1965), from which it was separated by Conn (1995).

*L. saxatilis* has been recorded from the Southern Lofty to the Northern Flinders Ranges (see Fig 2-6). According to Perry (1986), the species usually occurs on the rocky sides or floor of gorges. In the Southern Flinders Ranges, *L. saxatilis* is commonly found on open, elevated rocky slopes. It is restricted to South Australia.

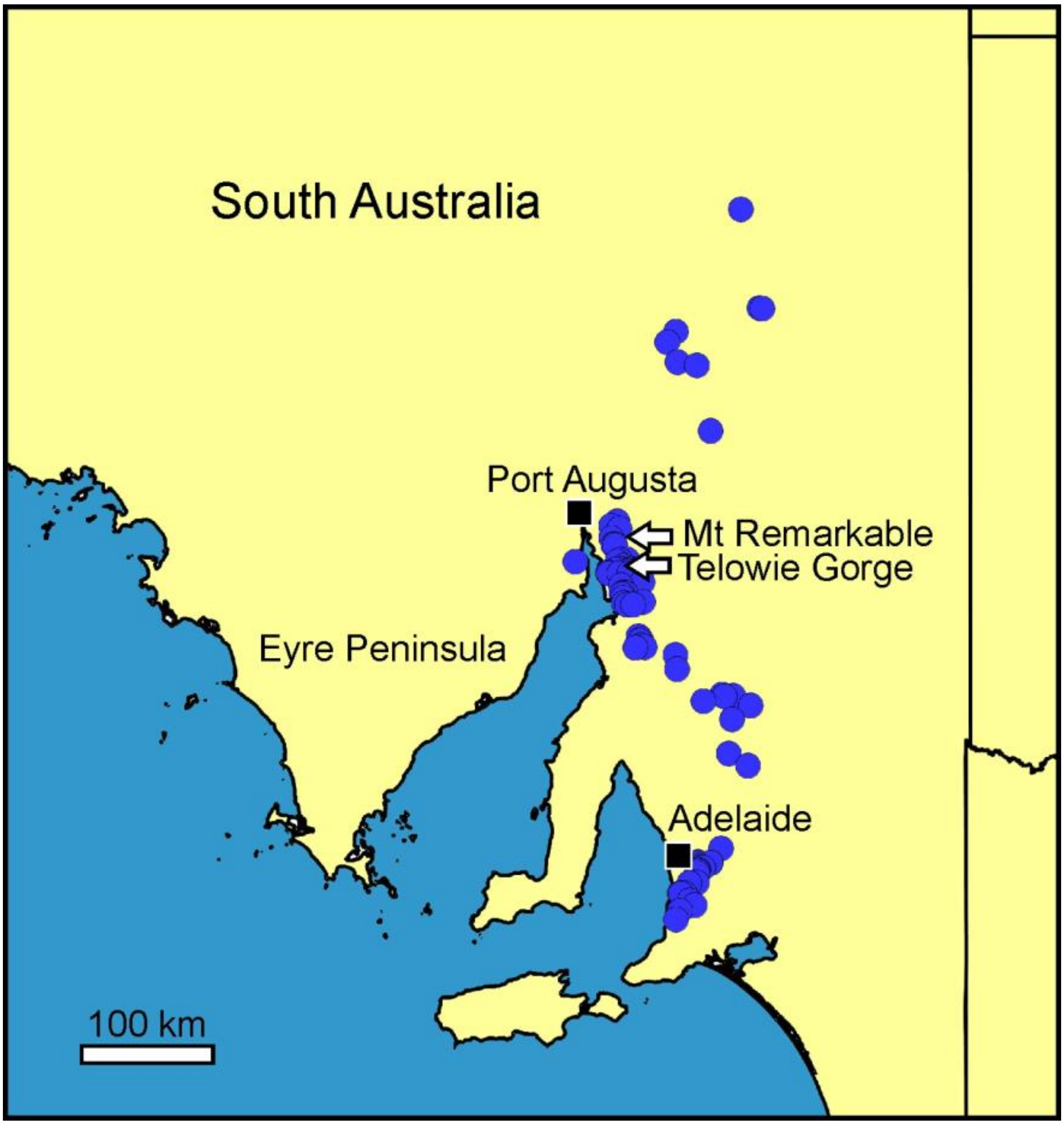


**Fig 2-6 Distribution of *Logania saxatilis* and the location of the two study sites in the Southern Flinders Ranges. Data from the Australian Virtual Herbarium (CHAH 2009 and ongoing).**

Conn’s (1995, 2013) detailed descriptions of *Logania saxatilis* forms the basis of the below account, with the addition of own observations.

The open, multibranched and often straggly shrubs are 1-2.5 m high with opposite and entire, glabrous, often glauceous (blueish), concave and ovate to elliptic leaves of 45-80 mm length. These sit on a distinct stem which is connected to its opposite by an interstipular membrane. The pennate venation and young stems are often yellowish. White unisexual, dioecious flowers arranged in attractive, multi-flowered terminal cymoses appear in spring (Fig 2-7, Fig 3-18). The flower is actinomorphic and has five petals, sepals and stamens, with a petal length of about four millimetres. The inside surface of the corolla tube is pubescent, and the staminal filaments of male flowers are inserted on a tube at about a third of their length. The style is simple, the ovary superior and two-celled, containing many ovules per cell.

**Fig 2-7 Flower of *L. saxatilis*, Mount Remarkable 2012**

The fruit is a dark capsule of about 4 mm length and width which is slightly contracted towards the summit where it opens (Fig 2-8). The seeds of *L. saxatilis* are brown, about 1 mm long, ovate, bilateral flattened with a concave and convex side each and a reticular pattern throughout the surface (Fig 4-4).

No information was found in the literature about the root system of *L. saxatilis*, but the root system of the closely related *L. vaginalis* was examined by Pate *et al.* (1990a) who found a tap root of

1.5 m length suitable for obtaining deep soil stored water resources. Lateral feeder roots extended near the surface. Three year old saplings of this species had a shoot: root ratio of 1: 5, approximately equal starch content in shoot and root, and a visually high density of starch grains in the root. These findings were considered to be more consistent with resprouters than with obligate seeders (Pate *et al.* 1990b).

For recruitment, some Loganiaceae germinate in response to various disturbances which increase the exposure of seed to light, and also to fire. Such is reported for *Mitrasacme* spp. in Australia (Benson 1985; Crosti *et al.* 2003; Kenny 2003), *Geniostoma rupestre* in New Zealand (Burrows 1999) and several species of *Buddleja* (Vàzquez-Yanes and Orozco-Segovia 1990; Mendoza-Hernández *et al.* 2010) which were previously included in Loganiaceae but are currently allocated to the Scrophulariaceae. Most of the above species have persistent seed banks that are dormant in the absence of light or fire. Conn (1995) reports the occurrence of *L. saxatilis* in small numbers in disturbed sites, but no information is available about its response to fire, and the matter does not seem to have been investigated (Conn, pers. communication 2013). However, for the closely related Western Australian species *L. vaginalis*, Archer (2011) reported recruitment after disturbance with or without fire. Closer examination of this species revealed that seeds were largely dormant without treatments, but germination increased to 20-30 % after exposure to smoke water (Shane Turner, Kings Park Botanic Gardens Perth, pers. communication 2013).

**Fig 2-8 Seedhead of *L. saxatilis*, Mount Remarkable National Park 2012**

Some other species related to *Logania* are reported not to thrive in the immediate post fire environment, or perhaps they require a different fire regime than observed. For example, a Northern Australian species of the *Mitrasacme* declined after fire (Russell-Smith *et al.* 2006), and an endangered Hawaiian *Spigelia* sp. did not appear to germinate at all for two years after fire (Ainsworth and Boone Kauffman 2009).

Vegetative responses after disturbances including fire have been reported for some species. Resprouting after fire was observed in *L. vaginalis* (Pate *et al.* 1990b). About 70% of *Logania albiflora* of NSW regrew after full leaf scorch (Bell 1998); and according to Benson and McDougall (1997), this species is a facultative resprouter. Post-fire resprouting was also observed in the herb *Mitrasacme polymorpha* (Kenny 2003). Some information is also available about time to maturity and longevity: *Logania centralis* B.J.Conn matures at the age of two to three years and has a lifespan of four to 20 years.

# 3 Fire response of Logania saxatilis populations

## 3.1 Abstract

South Australia's Mount Remarkable National Park and Telowie Gorge Conservation Park are home to the Rock Logania *Logania saxatilis.* Survey of the species to the age of up to 42 months after fire revealed that both resprouting and seedling emergence occurred. On one site, rapid resprouting was prevalent and accompanied by germination, while on the other, apparently extensive death of adults led to a population of seedlings alone. Some recruitment was also observed on unburnt sites, particularly at Telowie. Seedling mortality over summer was high and strongly density driven. It is concluded that *L. saxatilis* is a facultative resprouter, and that recruitment is promoted by fire. The regeneration pathway probably depends on fire regime and habitat quality, which together with aspects of plant size and phenology drive eventual fire severity and plant mortality.

## 3.2 Introduction

An indigenous shrub with a preference for elevated, rocky and open sites, the rare *Logania saxatilis* (Rock Logania) is known to occur in the Southern Flinders Ranges, north of Adelaide in South Australia. The Southern Flinders Ranges run approximately in a north-south direction, rising steeply from the plains below and consisting mainly of folded, ancient quartzite. Two biologically important parks in the region are Mount Remarkable National Park (Mount Remarkable) and Telowie Gorge Conservation Park (Telowie). Both reserves are managed by the Department for Environment, Water and Natural Resources South Australia (DEWNR, formerly DEH, Department for Environment and Heritage).

The land now included in Mount Remarkable National Park was formerly part of various pastoral leases, and it has grown from several smaller reserves to its current size of 16,000 ha (Bonython 1996). The Mount Remarkable Range, leading north from the summit, has been part of the park since 1972. Within this range, the study area is located in a near-ridge, deeply grooved and overall east-facing slope covered in *Eucalyptus goniocalyx* F.Muell. ex Miq. and *E. cladocalyx* F.Muell. mixed woodland and forest. Telowie covers nearly 2,000 ha and has been protected since 1970. It borders onto the sizable native forest reserves of Wirrabara Forest. At Telowie, the area of interest is an elevated, west to south west facing, open *Allocasuarina verticillata* (Lam.) L.A.S.Johnson woodland.

Sclerophyllous understorey in both locations includes *Xanthorrhoea quadrangulata* F.Muell., *Bursaria spinosa* Cav., various *Cassinia* and *Acacia* species, as well as *Logania saxatilis*. Telowie has a dense growth of *Lepidosperma sp.* Common herbivores include the Western Grey Kangaroo (*Macropus fuliginosus* Desmarest, 1817) and the Common Wallaroo or Euro (*Macropus robustus* Gould, 1841). The Yellow Footed Rock Wallaby (*Petrogale xanthopus* Gray, 1855) also occurs in both parks (Smith 1996), but is not known to visit the immediate area of the study sites.

In addition, Telowie harbours a sizable population of feral goats (*Capra aegagrus hircus* (Linnaeus, 1758)), but Mount Remarkable is considered to be free of goats (Smith 1996). Activity by rabbits (*Oryctolagus cuniculus* (Linnaeus, 1758) is also evident at Telowie.

Bushfires resulted in a complete burn of Mount Remarkable in 1988. At Telowie, wildfires affected the northern part in 1984, some of the southern in 1960 (Wirrabara Fire), but the remainder has no known history of fire (Department for Environment, Water and Natural Resources 2012b). Prescribed burning has increased in both reserves during the last few years, leaving some of the bushland in various stages of post fire recovery. At the commencement of this project, an autumn fire of about 500 ha size was planned for the range leading north from Mount Remarkable. This prescribed burn, scheduled for the end of March 2011, provided the opportunity for this study, and all field data collected about *L. saxatilis* at Mount Remarkable took place immediately before and during the two years after this fire.

It is important to note that in the two weeks prior to the above prescribed burn, over 100 mm of rain fell, representing three times the monthly average in this area of the state (Website of the Bureau of Meteorology, accessed on 30-11-2012).

At the beginning of the study in 2011, the Telowie study area was already regenerating from prescribed burn of approximately 70 ha applied on 22nd October 2009. This burn had taken place after a month of slightly above average rainfall, most of which had fallen about three weeks prior to the burn. While the fire was overall of low speed and intensity, observations on the day of burning suggest that the *Allocasuarina verticillata* woodland was subject to increased heat, as the fire moved quickly uphill towards it and intensified (Stuart Beinke, Regional Fire Management Officer DEWNR, pers. comm. 2012). Most *Allocasuarina* died as a result of the fire, and emergence of seedlings of many species was abundant, including numerous *L. saxatilis* shoots of 5–20 cm height within a dense growth of *Acacia continua* Benth., some *Pimelea microcephala* R.Br., and other species. Common resprouters included *Xanthorrhoea quadrangulata* and *Lepidosperma viscida* R.Br. *L. saxatilis* of various sizes and ages were also found in nearby bushland not been subject to recent (or any known) fire events. Since the conclusion of this study, the Bangor Fire of 2014 has affected most of Telowie, but not the 2009 burn site.

This part of the project investigates the post-fire recovery of *L. saxatilis* in the field and aims to answer following main questions:

- Do *L. saxatilis* populations survive fire, in particular prescribed burning?
- Is there a consistent pattern of responses across different sites in the Southern Flinders region?
- If populations survive fire, which regeneration strategies – resprouting or seedling growth – are observed, and which traits may allow morphological distinction in the field without destructive methods?
- Can any reasons for mortality be identified?
- Is fire beneficial for *L. saxatilis* through increased recruitment?

## 3.3 Methods

### 3.3.1 Site selection and monitoring method

Field monitoring recorded post fire abundance and growth characteristics of regrowth in areas where adult *L. saxatilis* were known to be present prior to burning. Mount Remarkable National Park was accessible immediately before a prescribed burn, and three sites located about 200 m from each other were chosen within the proposed burn area (Fig 3-2). These three sites were named MB1, MB2 and MB3. Their selection criterion was the presence of at least one female *L. saxatilis;* the gender was relevant in view towards securing a potential source of seeds. The female plant was marked with a loosely placed wire loop around its base to enable its identification after the fire. Additionally, the number and location of all *L. saxatilis* within an area of 24 × 24 m around this female were recorded. MB2 had a large population of adults of both genders, while the other two sites had only few adults in addition to the marked female. Due to time constraints prior to burning, more detailed measurements of habitat factors such as soil moisture and the location, species and size of other plants could not be taken.

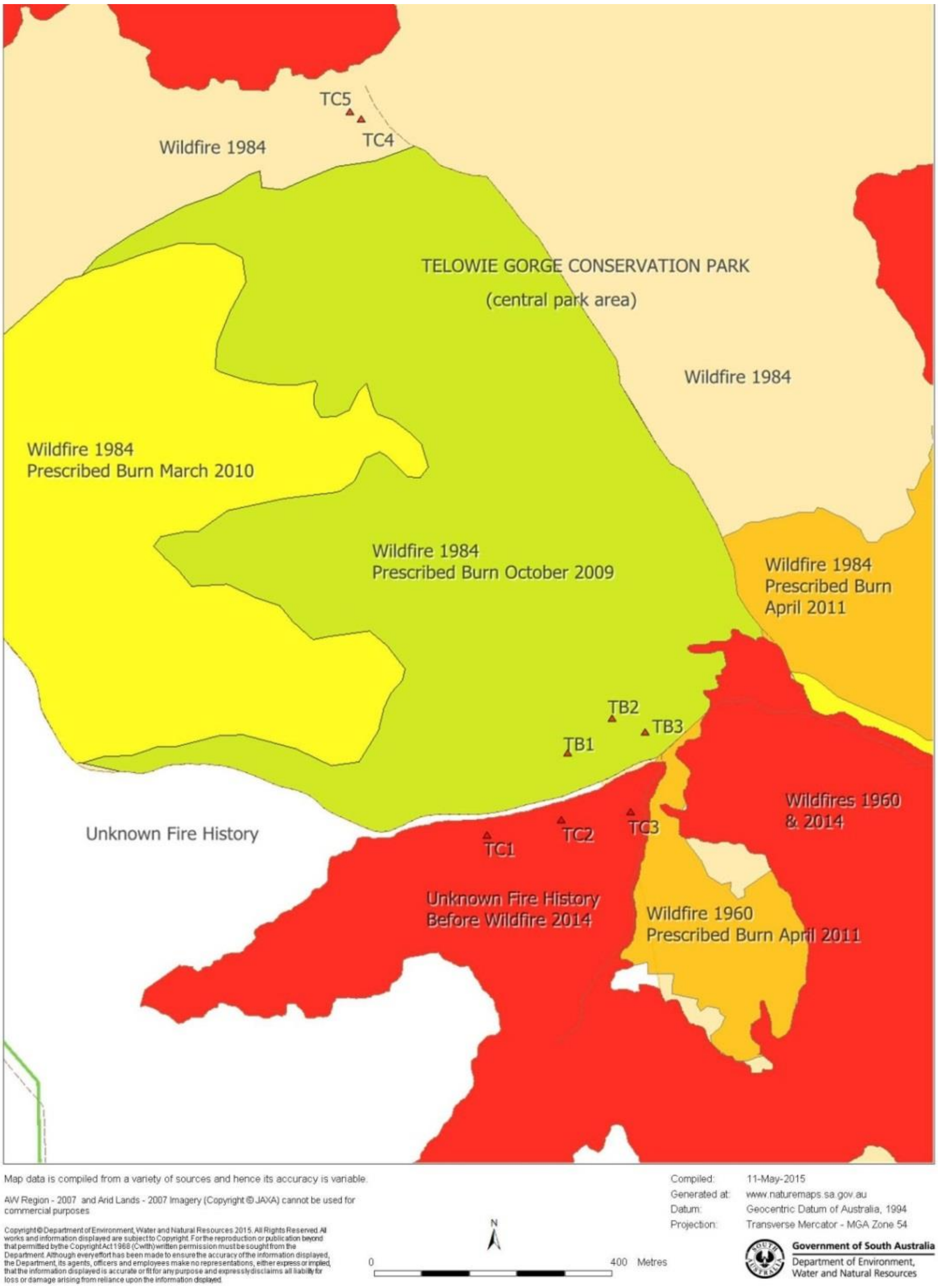
The prescribed burn took place as planned at the end of March/ early April 2011. A visual assessment after the prescribed burn confirmed that all sites had been suject to fire; scorched canopies remained on many burnt *L. saxatilis* shrubs. After the inspection, all sites were left undisturbed for three months; after this time, a number of 3 × 3 m quadrats for close observation were established on each site, resulting in a total of 48 quadrats. These quadrats always included the female *L. saxatilis* in a central position.

Given its larger population of *L. saxatilis*, 24 quadrats were installed on MB2, but 12 quadrats on each of the other two sites. The uneven, rocky and steep terrain did not allow for exact marking of quadrat boundaries, but corners of quadrats were clearly pegged. Therefore, some seedlings in marginal positions may not have been consistently allocated to the same quadrat; this may have potentially resulted in very minor variations of abundance not due to mortality. Five control sites were established in unburnt habitat along the range and named MC1 to MC5. These contained 12 quadrats each. Young plants or "seedlings" present on control sites were defined as plants with less than 10mm diameter at the soil surface.

**Table 3-1 Timeline of prescribed burns & post fire data collection at the two parks**

| | | | **Data collection (months post fire):** | |
|---|---|---|---|---|
| **Date** | **Season** | **Event** | **Telowie** | **Mount Remarkable** |
| October 2009 | Spring | Telowie Burn | | |
| March/ April 2011 | Autumn | Mt Remarkable burn | | 0 (pre-fire) |
| Aug/Sept 2011 | Spring | | 22 | |
| March/ April 2012 | Autumn | | | 12 |
| Aug/ Sept 2012 | Spring | | 36 | 17 |
| Oct 2012 -March 2013 | Summer | Seedling mortality | | |
| March/ April 2013 | Autumn | | 42 | 24 |

About five weeks after the fire, resprouting was confirmed through observation of young shoots emerging directly from scorched bases. No *L. saxatilis* seedlings were identified at this point in time, or later in winter/ early spring. Monitoring of both resprouts and seedlings took place in all quadrats 12, 17 and 24 months post fire (March/April 2012, August/September 2012 and March/April 2013, see Table 3-1). Monitoring included: abundance of *L. saxatilis* shoots (seedlings as well as resprouts); height of shoots in 5 cm increments; distance of shoots to the scorched bases of adults, in 10 cm increments, with regrowth emerging directly on burnt stumps recorded as a distance of 1 cm, and distances of 350 cm and more pooled; vigour by colour and integrity of leaf in three classes 1-3, with green considered as indicator of the highest vigour (3), some damage and /or discolouration to be second (2), and leafless and/or apparently dead seedlings as "dead" in lowest vigour class (1); leaf length as an indicator of vigour and progress towards maturity, in two classes under 50 mm (1) and over 50 mm (2) including stalk; reproductive status – presence (2) or absence (1) of any of the following: buds, flowers, or fruit related structures. Presence of any of the above was considered to be the onset of maturity regardless of the size of the plant; the term "flowering" is used synonymously for "maturity" hereafter. Where applicable, grouping of seedlings was also recorded: individuals with a continuity of overlapping leaves were considered to be grouped. Regeneration through seedlings was confirmed by carefully excavating the root system of twelve shoots outside the monitoring quadrats to avoid disturbance and impact on abundance. By subjecting all the above morphological data from Mount Remarkable to ordination (see Data Analyses), it was tested whether or not the two growth forms could be distinguished without the requirement to excavate. It was decided not to measure stem diameter of regrowth to avoid excessive handling, as it may potentially have resulted in tissue damage, and affected experimental results.



Map data is compiled from a variety of sources and hence its accuracy is variable.

AW Region - 2007 and Arid Lands - 2007 Imagery (Copyright © JAXA) cannot be used for commercial purposes

Compiled: 11-May-2015
Generated at: www.naturemaps.sa.gov.au
Datum: Geocentric Datum of Australia, 1994
Projection: Transverse Mercator - MGA Zone 54

**Fig 3-1 Location of field sites at Telowie Gorge CP with fire history (different fires are colour-coded): TB1-TB3 indicates the location of experimental (burnt) sites, TC1-TC5 the corresponding (unburnt) control sites. Created with the online mapping tool "Naturemaps" and reproduced with kind permission of the Department of Environment, Water and Natural Resources South Australia (DEWNR).**

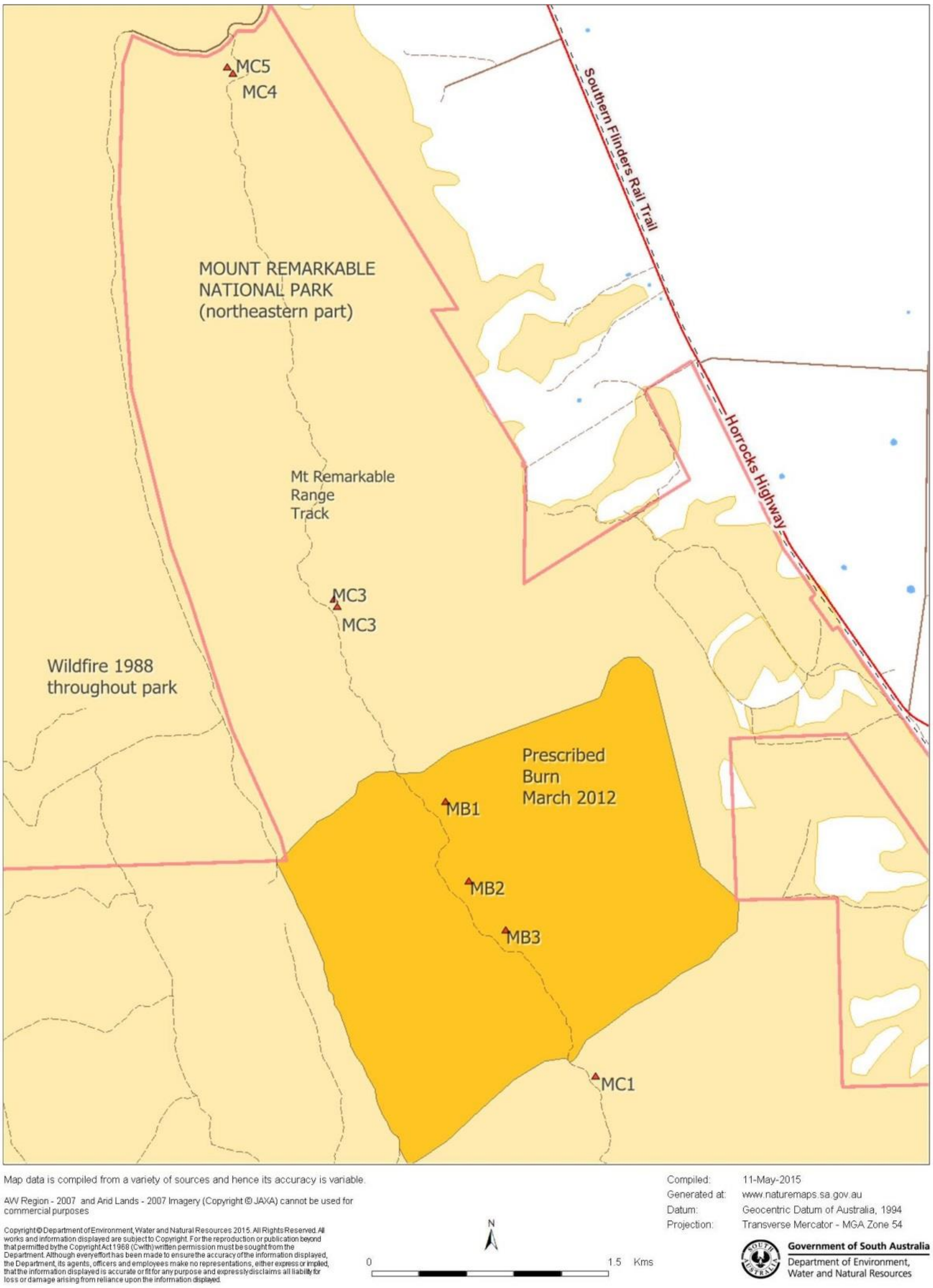


**Fig 3-2 Location of field sites at Mt Remarkable NP with fire history (different fires are colour-coded): MB1-MB3 indicates the location of experimental (burnt) sites, MC1-MC5 the corresponding (unburnt) control sites. Created with the online mapping tool "Naturemaps" and reproduced with kind permission of the Department of Environment, Water and Natural Resources South Australia (DEWNR).**

At Telowie, three sites (TB1–TB3) at different elevation along the west facing slope were selected for presence of *L. saxatilis* shoots and divided into quadrats as above (Fig 3-1). Abundance of shoots was recorded. Due to the enormous number of *L. saxatilis* shoots within some of the above quadrats, closer observations were recorded at 2 m intervals along a 30 m transect through each site, on permanently marked small quadrats of 35 × 35 cm at 2 m distance from each other; here, given the smaller amount of plants monitored, they were marked with loosely fitting plastic rings around the base; the same measurements as for the quadrats at Mount Remarkable were taken. Within these small quadrats, genus, abundance and height of other shrub species was also recorded. Five control sites were set up in the surrounding unburnt bushland carrying a mixture of sizes and apparent ages of *L. saxatilis* (TC1–TC5) and monitored in the same manner. Due to the much lower density of seedlings, these observations all related to 3 x 3 m quadrats.

Although by the end of the study most seedlings had approached a stage more appropriately described as sapling, for simplicity all growth apparently originated from seed will be referred to as seedlings in this text, irrespective of height and leaf stage.

### 3.3.2 Data analyses

During the collection of data, it became obvious at an early stage that the regrowth at Mount Remarkable represented two distinctly different groups, namely resprouts and seedlings, while regrowth at Telowie appeared to a more uniform population consisting entirely of seedlings. To test whether or not the monitoring method would also distinguish between seedlings and resprouts by representing them as two separate groups, the data collected at Mount Remarkable 12 months post fire were subjected to multivariate cluster analysis using PC-Ord 4.0 (McCune and Mefford 1999) with relativised Euclidean Distance and Ward's Method association to produce a dendrogram after $\log_{10}$ transformation of the data. A two-dimensional ordination plot was produced using non-metric multidimensional scaling (see Fig 3.3). This did indeed confirm the presence of two distinct main groups at Mount Remarkable. Data from Telowie referred to a single group of regrowth - seedlings - with particularly height and leaf size being more uniform and representing an approximately normal distribution around a single peak (Fig 3-5). It was therefore decided not to conduct a multivariate analysis for the Telowie data.

Further investigations into growth and survival over time were applied to the three groups separately: Resprouts at Mount Remarkable, seedlings at Mount Remarkable, and seedlings at Telowie. Using single factor ANOVA in Excel, these investigations searched for significance ($p<0.05$) of the changes in abundance, average vigour, height and leaf size during the two years of the study. For seedlings alone, the occurrence in groups (defined by overlap of canopies) and their distance to the closest adult were analysed in the same manner.

To illustrate the profound differences between seedlings and resprouts growing in close proximity on one site, and the similarity of seedlings across the two parks, some growth and survival data of the different groups are presented in the same graphs.

## *3.4 Results*

### *3.4.1 Population survival and consistency of response*

Population survival and recovery through abundant seedling growth, and variably through rapid resprouting, were recorded on all burnt sites. Burnt sites had many more seedlings than unburnt control sites. Resprouts formed tall, multistemmed growth which emerged from burnt stumps, while seedlings were smaller plants with individual tap roots that had no connection to older or scorched plant matter. At Mount Remarkable, both forms were found, but Telowie appeared to carry only seedlings, which were taller than the ones at Mount Remarkable, as it could be expected from the differences in age since fire. The two parks also varied in the abundance of young growth on unburnt control sites. The height data collected for control sites showed that on the Mount Remarkable control sites, only two plants considered juveniles were located, while at Telowie, a large number of apparently young plants with a stem diameter less than 10mm and a wide range of heights were found (Fig 3-6).

These two forms of post-fire regrowth were distinctly different in the field and as already outlined in the Methods, this was confirmed by the multivariate analysis of the data collected 12 months after fire (Fig 3-3). Resprouts had much greater height and leaf size. Seedlings, which emerged at some distance from burnt adults, were small in both height and leaf size. The clear distinction in size at this age is also apparent in the height distributions: the Mount Remarkable growth is divided into two separate distributions 12 months after fire (Fig 3-4), while the Telowie growth is clustered around a single peak. Vigour, while initially somewhat greater in resprouts than in seedlings, was less suited to distinguish the two growth forms.

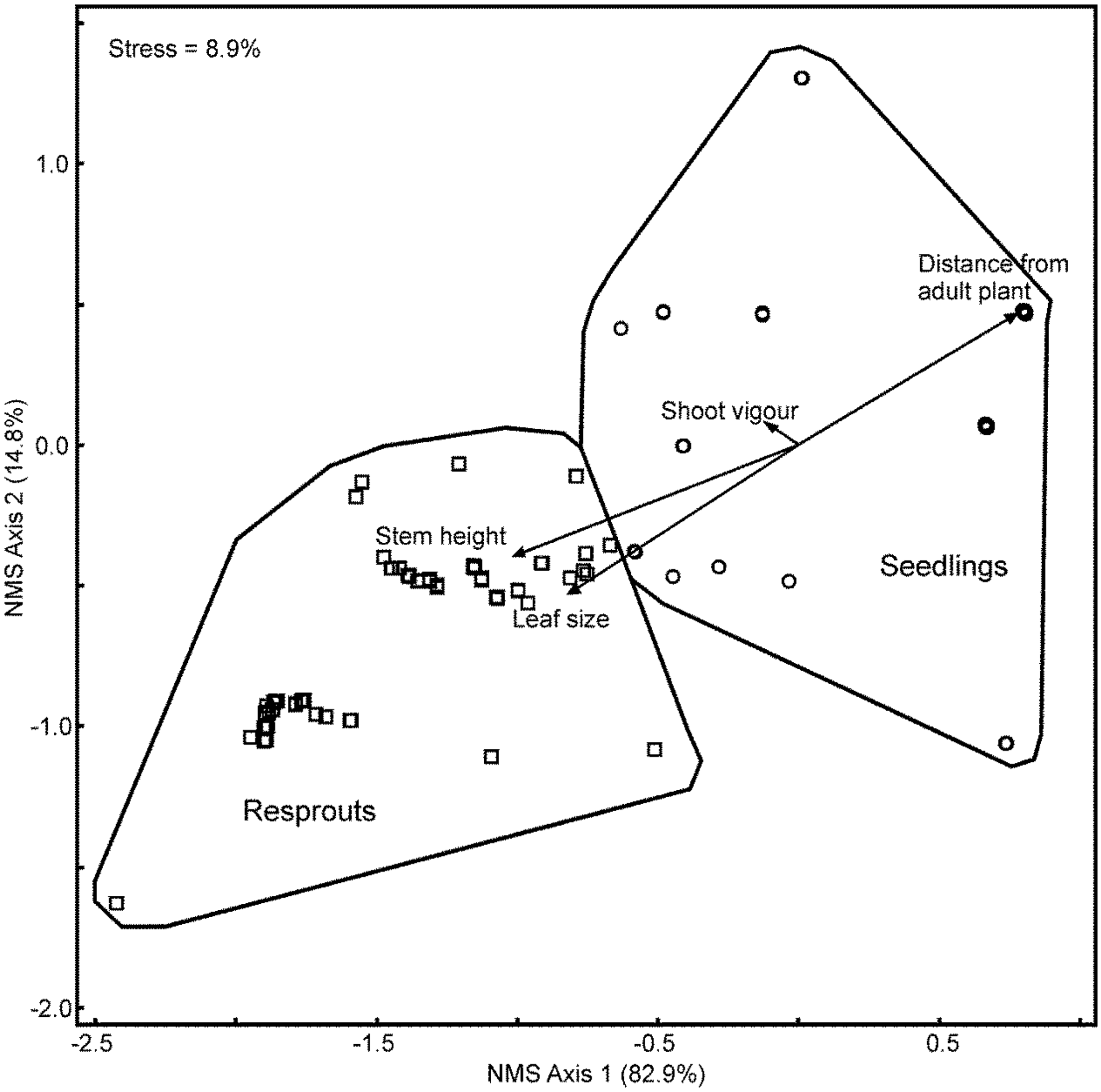


**Fig 3-3 Non-metric multidimensional scaling ordination of regrowth by *L. saxatilis* measured across all sites at Mount Remarkable 12 months after fire, showing the two different regeneration strategies (seeding and resprouting). Relative Euclidean Distance/Ward's Method cluster analysis and their relationship to morphological characteristics as indicated by Principle Canonical Correlation vectors. Percentages indicate the amount of variance explained by each axis. Group 1 represents seedlings, group 2 the resprouting adults.**

Resprouts and seedlings were not only morphologically different from the first data record, but also performed differently over the remaining study period in matters such as survival, growth rate and time to maturity.

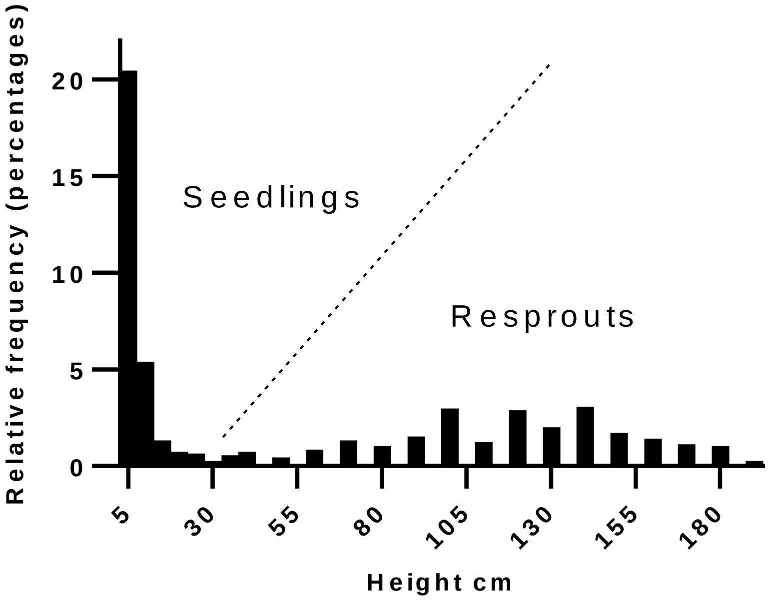


Fig 3-4 Height of regrowth approximately 17 months post fire is divided into two distributions at Mt Remarkable

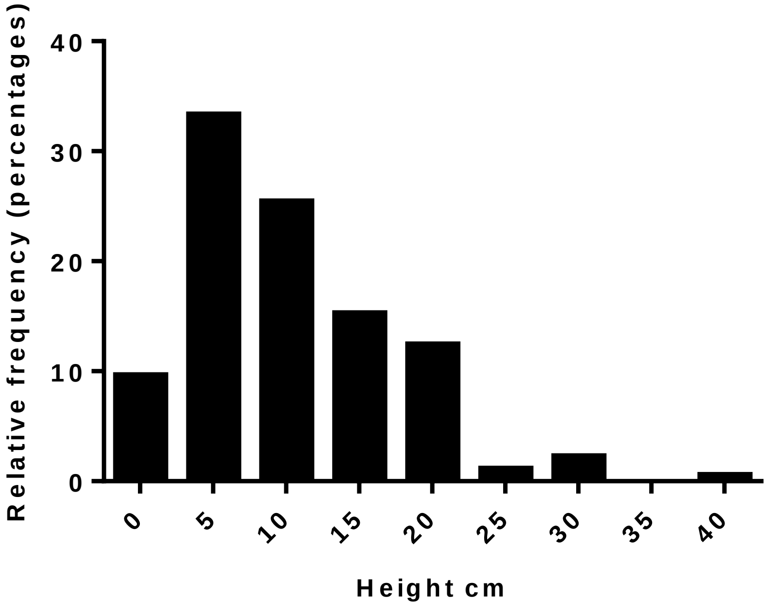


Fig 3-5 Height of regrowth at Telowie 18 months after fire forms a distribution around a single peak

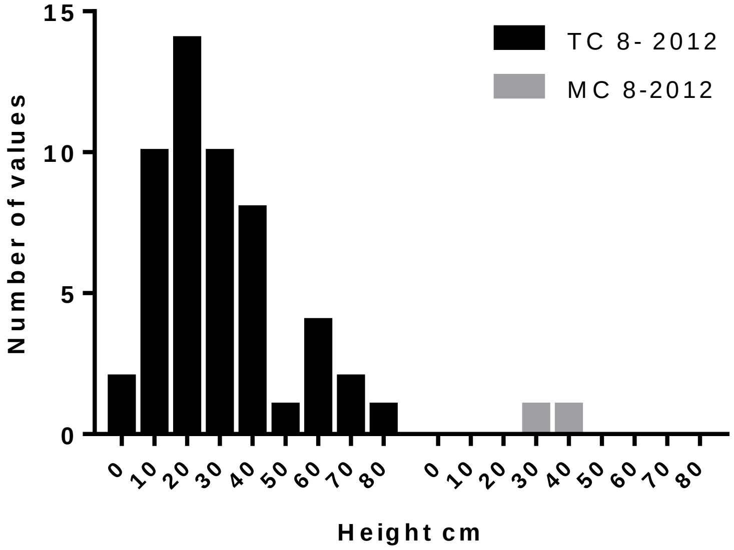


**Fig 3-6 Height distribution and abundance of juveniles on unburnt control sites (C) at Mount Remarkable (M) and Telowie (T) in 2011**

### *3.4.2 Traits and performance of resprouting adults*

Twelve months after fire, the 16 resprouts at Mount Remarkable had an average of 13 shoots with a mean height of 103 cm each; each shoot emerging directly from the base provided further information on leaf size, vigour and maturity. Mean height reached its peak at 17 months age. Leaf size was over 50mm at 12 months after fire and remained unchanged. Vigour was relatively high at 12 months but then dropped significantly, particularly due to yellowing of foliage during the remainder of the study. Return to maturity through flowering was recorded for nearly all resprouting adults at 17 months post fire, and evidence of seed production (presence of dry seedheads) was observed at 24 months. Importantly, no mortality occurred amongst the resprouting *L. saxatilis* adults (Fig 3-9).

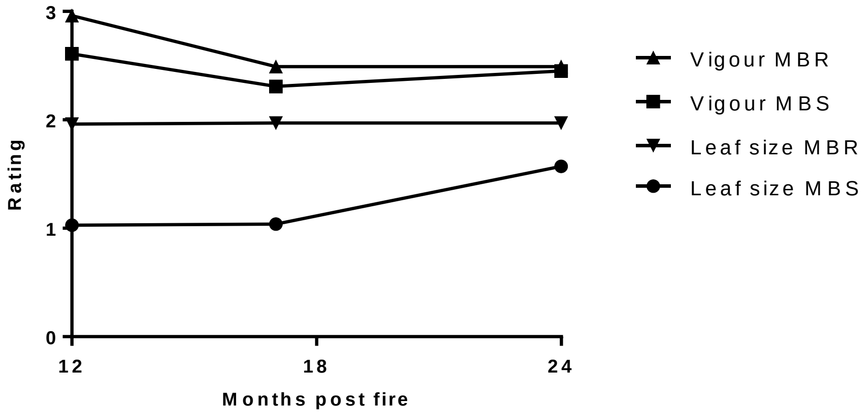


**Fig 3-7 Size (1 small, 2 large) and vigour (2 discoloured/severely damaged, 3 green) of leaves in live seedlings (S) and resprouts (R) on burnt sites at Mount Remarkable (MB). Resprouts had adult sized leaves from the first assessment, while seedlings initially all had small leaves, but the mean leaf size increased in the surviving seedlings.**

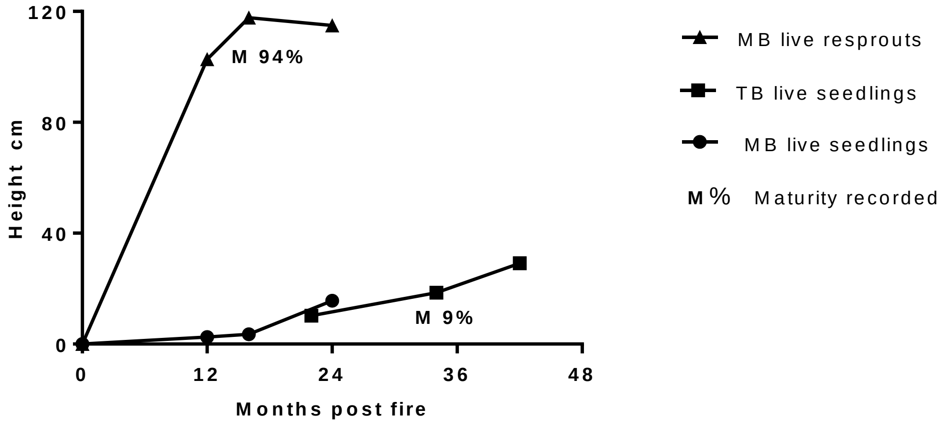


**Fig 3-8 Comparison of height between resprouts and seedlings on burnt sites at Mount Remarkable (MB) and at Telowie (TB). The position of M indicates the point in time when flowering was first recorded, and the proportion of flowering individuals is expressed in %.**

**Fig 3-9 Abundance of growth forms at both sites: all *L. saxatilis* resprouts (R) at Mount Remarkable burnt sites (MB) survived, but there were very high losses of seedlings (S) in summer 2012/13 (←S→). On the burnt sites at Telowie (TB), which had older seedlings and no resprouts, losses during the same time were still high, similar to other shrub species the same sites (TBO) and to L. saxatilis on unburnt (TC) sites; age is given in months since fire.**

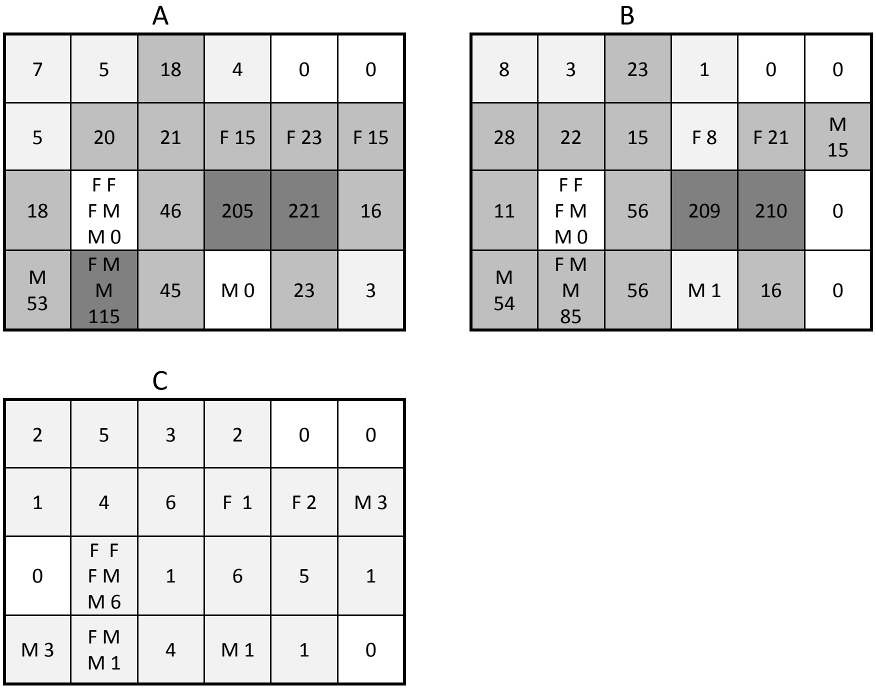
**Table 3-2 Statistical significance of trait changes in regrowth on the burnt sites over time (single factor ANOVA in Excel) SS Sum of Squares; NS not significant; p≤0.05**

| | **Change at MB 12 to 17 months (winter)** | | | | **Change at MB 17 to 24 months (summer 2012/2013)** | | | | **Change at TB 34-42 months (summer 2012/2013)** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **SS** | **Total SS** | **Df** | **p** | **SS** | **Total SS** | **Df** | **P** | **SS** | **Total SS** | **Df** | **P** |
| **Resprouts** | | | | | | | | | | | | |
| Height | 24017 | 598276 | 1 | p<0.001 | 867 | 553272 | 1 | NS | | n/a | | |
| Vigour | 27 | 82 | 1 | p<0.001 | 0.0003 | 101 | 1 | NS | | | | |
| Leaf size | 0.001 | 18 | 1 | NS | 0.0001 | 12 | 1 | NS | | | | |
| **Seedlings** | | | | | | | | | | | | |
| Height | 429 | 43053 | 1 | p<0.001 | 13913 | 57131 | 1 | p<0.001 | 2041 | 50502 | 1 | p<0.001 |
| Vigour | 37 | 441 | 1 | p<0.001 | 2 | 201 | 1 | NS | 85 | 222 | 1 | p<0.001 |
| Leaf size | 0.076 | 55 | 1 | NS | 11 | 119 | 1 | P<0.001 | 2 | 54 | 1 | NS |
| Distance to adults | 95596 | 17937461 | 1 | NS | 630851 | 10904468 | 1 | p<0.001 | | n/a | | |

### *3.4.3 Traits and performance of seedlings*

Seedlings emerged in great abundance after the fire: a total of 950 live seedlings were found 12 months after the burn on the 48 quadrats at Mount Remarkable. The maximum recorded density was 221 seedlings per 3x3 m quadrat, in comparison to 438 seedlings at Telowie. As mentioned above, unburnt control sites in this park carried over 50 apparently young recruits of less than 10 mm diameter, while only two were found at Mount Remarkable. Mean height of seedlings at Mount Remarkable was only 2.6 cm when first recorded at 12 months age. However, growth occurred in both parks throughout the two years of the study; height rose sixfold at Mount Remarkable, while the older and already taller seedlings at Telowie nearly tripled in size. In the end, Mount Remarkable seedlings were approximately the same age and height as the Telowie seedlings had been at the start of the project (Fig 3-8).

Seedling vigour at Mount Remarkable dropped significantly over winter from 12 to 17 months post fire, but not during the following summer (Table 3-2). Leaf size rating in this park was initially mostly low, but increased significantly after 17 months over summer (Fig 3-7, Table 3-2). In the older seedlings at Telowie, height significantly rose over summer, while vigour ratings dropped (from a mean of 2.82 to 2.44); leaf size increased slightly (1.55 to 1.75). Maturity was first observed at Telowie in 2012, when 11 of the then 173 young plants (Fig 3-8) flowered. It is important to assess these changes in traits in association with the high mortality in summer (see Discussion).



A

| | | | | | |
|---|---|---|---|---|---|
| 7 | 5 | 18 | 4 | 0 | 0 |
| 5 | 20 | 21 | F 15 | F 23 | F 15 |
| 18 | F F<br>F M<br>M 0 | 46 | 205 | 221 | 16 |
| M 53 | F M<br>M 115 | 45 | M 0 | 23 | 3 |

B

| | | | | | |
|---|---|---|---|---|---|
| 8 | 3 | 23 | 1 | 0 | 0 |
| 28 | 22 | 15 | F 8 | F 21 | M 15 |
| 11 | F F<br>F M<br>M 0 | 56 | 209 | 210 | 0 |
| M 54 | F M<br>M 85 | 56 | M 1 | 16 | 0 |

C

| | | | | | |
|---|---|---|---|---|---|
| 2 | 5 | 3 | 2 | 0 | 0 |
| 1 | 4 | 6 | F 1 | F 2 | M 3 |
| 0 | F F<br>F M<br>M 6 | 1 | 6 | 5 | 1 |
| M 3 | F M<br>M 1 | 4 | M 1 | 1 | 0 |

**Fig 3-10 A-C: Location and abundance of seedlings (arabic numerals) and resprouts (letters F female, M male) in quadrats on burnt site number two (MB2) at Mount Remarkable over time : (A) 12 months post fire in April 2012, (B) 17 months post fire in September 2012, and (C) 24 months post fire in April 2013. Site slopes steeply from top row to bottom and less so from left to right, with an effect on seed placement and seedling density in relation to adults. Further adults were located in the wider surroundings of the site.**

### 3.4.4 *Mortality of seedlings*

At each count, some mortality was documented at Mount Remarkable. Losses of 15 % occurred during the winter of 2012. Mortality during the following summer was very high and resulted in a survival rate of just 10 % since the initial count (Fig 3-9). A single seedling remained on the Mount Remarkable control sites. Transect monitoring at Telowie recorded a mortality of 35 % of all shrub seedlings over the same summer. Several aspects of seedling positioning were connected to seedling abundance over time. Mortality was strongly driven by very substantial thinning in the quadrats with the greatest initial seedling numbers. On site MB2, these were located downhill of female adults (see map of seedlings and resprouts in Fig 3-10). There was a clear negative relationship between initial seedling abundance and survivorship at this site (Fig 3-11).

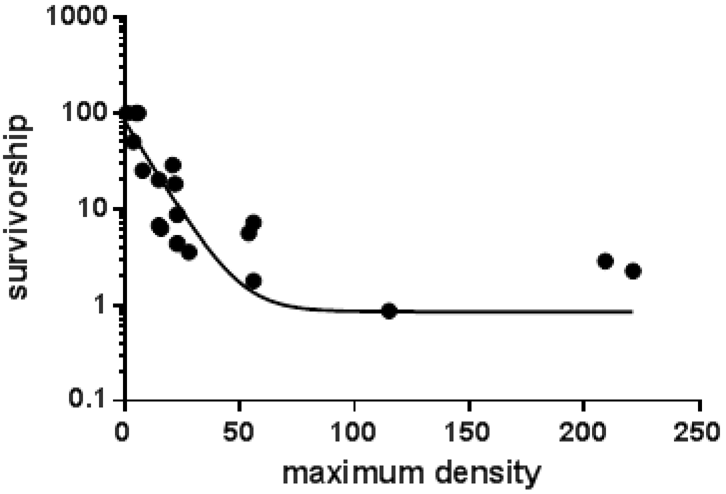


**Fig 3-11 Mortality of seedlings at site MB2 was clearly connected to their initial density within the 3x3 m quadrats**

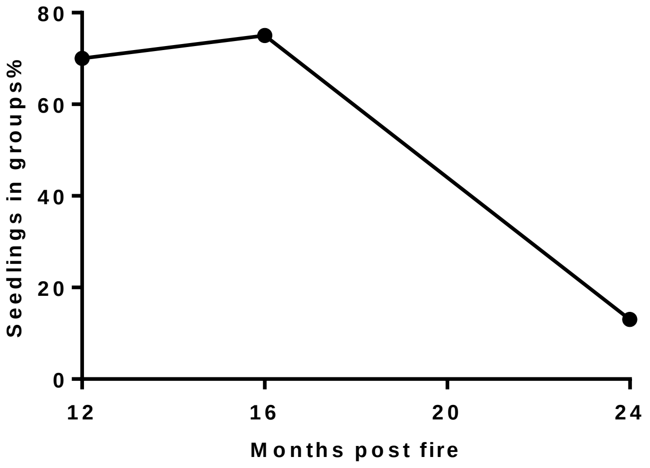


**Fig 3-12 Percentage of live grouped seedlings of all live seedlings on burnt sites at Mount Remarkable declined sharply during the dry summer 2012/13.**

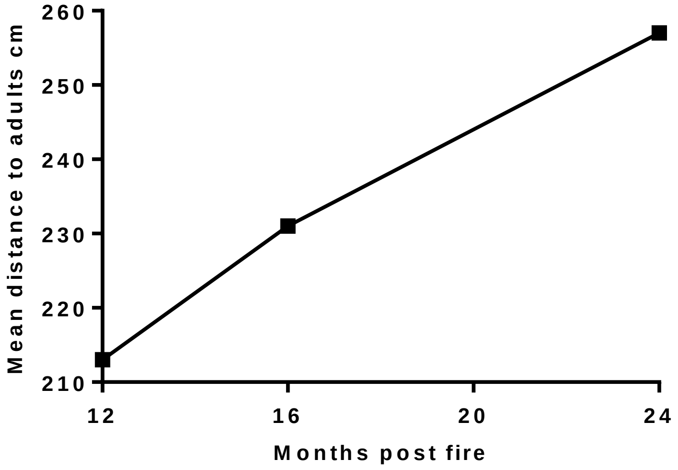


**Fig 3-13 Mean distance of surviving seedlings to adults increased at Mount Remarkable, due to higher mortality of seedlings closer to adults.**

In addition, there was a strong decline of grouped seedlings, which again suggests density-dependent mortality. Twelve months after fire, 70% of live seedlings at Mount Remarkable were grouped and 30% were placed singly. However, at the age of 24 months and after a dry summer, only about 13% of live seedlings remained grouped (Fig 3-12), a disproportionally steep decrease even in comparison with the overall high mortality.

Thirdly, proximity to conspecific resprouting adults reduced survival (Fig 3-13). The mean distance of live seedlings to resprouting adults was 213 cm at 12 months post fire, rose to 231 cm at

17 months, to eventually reach 257 cm two years after the fire; these were all significant increases in ANOVA and clearly demonstrate a negative effect of adults on closely located seedlings. Average distance of grouped seedlings was 115, 226 and 292 cm accordingly. The difference in distances to adults between the grouped population and the overall seedling population was not significant in ANOVA.

## 3.5 Discussion

### 3.5.1 General fire response

The rapid return of resprouting adults to maturity and the profuse seedling emergence reveal a strong adaptation of *L. saxatilis* to fire related disturbance. Fire events at the observed intervals of over 20 years, including the application of prescribed burning, are not a threat to the species, but can be viewed as beneficial to population recruitment. The two growth mechanisms resprouting and seedling recruitment are both well developed and successful strategies in the post fire recovery of this species. In the first two years of regrowth the two plant forms clearly differed in a number of ways such as height increase, leaf size, survival rate and vigour. These differences should allow distinction in the field without the requirement to apply invasive methods (such as excavation) that may incur the loss of individuals of this rare species. The inconsistency of the resprouting response characterises *L. saxatilis* as a facultative resprouter (Thomas and Davis 1989; Benwell and McCorkell 2011). As such, *L. saxatilis* is similar to the closely related *L. vaginalis* (Labill.) F.Muell. in Western Australia (Archer 2011); it also shares traits with *L. albiflora* (Andrews) Druce (Benson and McDougall 1997; Bell 1998), and with *L. centralis* B.J.Conn, (Gardener and Morrinan 2007).

### *3.5.2 Traits and trajectories of resprouting*

Resprouting adults of *L. saxatilis* in this study were characterised by rapid growth of multiple shoots with adult sized leaves (over 50 mm length) from the plant base (Fig 3-14, Fig 3-15). The resprouting response represented an enormous production of biomass, given the recorded average of 13 shoots of a mean length of 103 cm is equivalent to a total shoot elongation of about 13.4 m per plant. The rapid canopy growth ensured priority access to further resources, in particular light (Falster and Westoby 2005) ahead of potential competitors, and also at the expense of conspecific seedlings.

The regrowth process was completed by 17 months and immediately followed by reproduction, finalising the rapid return to the pre-fire, established adult population. Therefore, readily available seed, such as it may have been stored in a soil seedbank, and reduced or removed after germination, can start to be replenished within two years of the fire, and provided that seed can maintain viability after dispersal, or fruiting is repeated yearly, resilience to another major disturbance is progressively rebuilt.

This behaviour confirms findings by Vivian and Cary (2012) that facultative resprouters follow a strategy of rapid regrowth and resource acquisition. Soil resources could be accessed immediately by the established root system (Thomas and Davis 1989). Given that starch storge has been demonstrated for the closely related *L. vaginalis* (Pate *et al.* 1990b), it can also be speculated that such a resource may also be present in *L. saxatilis* and contribute to the rapid early recovery, although this would require further study (see “Further Research”). The enormous growth potential of resprouts lends them a great advantage over young seedlings that have to pass through the early stages of growth and establishment in competition with adults and other species. Such ability to recover from canopy damage may render the species a valuable component of rangeland grazing, provided the leaves are non-toxic and palatable to stock, and grazing managed to allow

**Fig 3-14 Resprouting *L. saxatilis* at Mount Remarkable, April 2012**

sufficient time for plant recovery. This potential economic relevance of *L. saxatilis* could be investigated in a further study (see “Further Research”).

However, such fast growth must also place great demands on the metabolism of *L. saxatilis* plants, and it can be speculated that plant and soil stored nutrients were much reduced as a result, quite possibly taking some time to be replenished to the pre-fire level. Such lack of available nutrients as might be expected from the rapid growth may be the reason for the yellowing recorded from the age of 17 months onwards. A variation in nitrate availability, also found to be relevant to germination (see Chapter Four), may be involved here. This apparently stressed state, which may interfere with further growth, could indicate sensitivity of the resprouting potential to high fire frequency (Hodgkinson 1998) or other major disturbances that occur in quick succession and lead to loss of the recently replaced canopy. As outlined above, grazing for excessive periods of time can be expected to have a similarly negative effect.

**Fig 3-15 Base of resprouting *L. saxatilis* at Mount Remarkable about 14 months after fire**

While resprouting was prominent at Mount Remarkable, no resprouts were found at Telowie, and it is concluded that all adults were killed in the fire, after which the population regrew from seedlings alone.  This recorded inconsistency of resprouting from park to park calls for an explanation. Plant size may play a role in survival, as it clearly varied between the parks. A greater occurrence of smaller growth (less diameter and height), presumed to be juveniles,was documented at Telowie (Fig 3-6). Generally, smaller diameter plant stems are more easily heated and killed by fire, so all other things being equal, fire severity can be expected to be greater in a population of smaller individuals. If adults were in general of smaller size at Telowie than at Mount Remarkable, then mortality due to direct scorching and burning can be expected to have been been greater at Telowie. In addition to plant ecotype and size, many external impacts are directly linked to fire severity and resprouting capacity, but these were not the focus of this study and their involvement can only be speculated upon.  Such external factors include for example weather (Bradstock *et al.* 2009). Weather data are available for both sites, and it can be established that the conditions at the time of both fires favoured resprouting capacity at Mount Remarkable over Telowie due to differences in precipitation: At Telowie, low rainfall and sunny conditions in the weeks leading up to the fire had a drying effect on the more or less west facing sites, providing favourable conditions for burning. However, at Mount Remarkable above three times the monthly average of rain fell in the two weeks prior to the fire, much contributing to soil moisture content which possibly later reduced fire severity (Bond and Van Wilgen 1996) and promoted plant recovery: presence of soil moisture is a crucial and widely recognised factor in resprouting ability (Benwell 1998; Hodgkinson 1998; Benwell 2007; Moreira *et al.* 2012).

Other generally known contributors to fire intensity and severity are for example surface fuel amounts (Agee and Skinner 2005) and fire season (Knox and Clarke 2006). It can be speculated that these factors were involved in a higher mortality of *L. saxatilis* at Telowie. Fuel was not measured, but the dense undergrowth of *Lepidosperma* and other low dense plants at Telowie was noticeable and provided ample finely structured, well aerated fuel (Whelan 1995), while soil surfaces at Mount Remarkable were generally more rocky and bare. Potential differences in the resprouting ability of shrubs between spring and autumn fires may be relevant (Rundel *et al.* 1987), possibly in connection to starch storage, an important resource for reprouting. However, these matters were outside the scope of the current study; avenues towards such investigations are outlined in more detail in “Further Research”. All that can be established with certainty is that given the inconsistency of resprouting, it can be expected that in response to prescribed burns, some *L.saxatilis* populations will resprout, while in others survival will depend on successful establishment of recruits from seed. Survival and performance of resprouted adults beyond the first two years after fire are not known; the observed yellowing of foliage points towards the possibility of a decline of resprouts at some time after fire.

### *3.5.3 Traits and trajectories of seedlings*

Strong seedling emergence led to a large number of new *L. saxatilis* individuals on all burnt sites, far exceeding the count on unburnt sites (Fig 3-16). Disturbance by fire clearly had a very strong positive effect on germination and emergence. It was not clear from the field study exactly which fire-related factor triggered the strong emergence of seedlings, and laboratory testing of seed was later undertaken to clarify this matter and determine the specific role of fire in the recruitment of *L. saxatilis* (see Chapter 4) There was some inconsistency in the strength of recruitment in the absence of any fire within the habitat: on unburnt control sites at Telowie, many more young plants were found than at Mount Remarkable. Seedling growth was slow and seedlings could be identified by being single stemmed, immature individuals of mostly low height and small leaf size 12 months after fire. Seedling height related to age was similar in both parks in spite of the many differences in the vegetation community, aspect, fire season and severity, and in resprouting response. Seedling mortality was high, as commonly observed in mediterranean habitats (Navarro and Guitián 2003).

**Fig 3-16 *L. saxatilis* seedlings at Mount Remarkable 12 months after fire**

At Mount Remarkable, seedling mortality was accompanied by a drop in vigour during autumn and winter 12-17 months post fire, when apparent insect and fungal attack were observed. However, mortality was highest during summer, probably driven by seasonally dry conditions between 17 and 24 months after fire. After this time, the remaining live seedlings encountered in March 2013 had higher vigour ratings, greater height and larger leaves than the population during the previous winter (Fig 3-7), probably as a result of mortality of smaller and weaker seedlings in a selection process that favoured better developed individuals. Seedlings were also affected negatively by crowding and proximity to adults. All these are known causes of seedling death (Lamont *et al.* 1991; Navarro and Guitián 2003; Castro *et al.* 2004; Moles and Westoby 2004). At Telowie, mortality during summer drought was similar to *L. saxatilis* on control sites and the same as in post fire emerged obligate seeders of genera such as *Acacia, Eutaxia, Melaleuca, and Pimelea*). The selection process towards the seedlings of greater height and larger leaves was similar to the process at Mount Remarkable.

Given the great density of seedlings on both sites, it is likely that a large proportion of the available seed had germinated under the influence of fire, probably after having been previously stored in a soil seed bank (Rawson *et al.* 2013). The view that in the absence of fire, seed may retain viability for more than one growth season is supported by the results of the germination study, which followed the field study. In this second experiment, very high germination rates of two year old seed were recorded after the exposure of seed to fire-specific triggers (see Chapter Four). It follows that repeated failure of seedlings on sites where adults had perished could lead to seed bank depletion, decline of the species and dependence on seed dispersal into the site from other populations. In remnant vegetation within a fragmented landscape, such dispersal from other sites may not be possible, resulting in local extinction (Croft *et al.* 2010).

According to Clarke *et al.* (2009), the minimum threshold for fire frequency in temperate regions is the length of the primary juvenile period (time to maturation) plus three years for accumulation of sufficient seed in the soil. In *L. saxatilis*, maturation was first observed in some of the three year old seedlings; however summer drought led to large plant losses, interfering with successful maturation of the population and seed bank replenishment. A minimum fire interval of six years, calculated using the above method, is therefore not likely to be sustainable for *L. saxatilis* in its semi-arid environment; rather, the observed processes and mortality during drought highlight the relevance of benign conditions for regrowth post fire.

### *3.5.4 Density-dependent effects on seedling survival*

All three measurements of spatial arrangements of the seedling population provided evidence of negative density dependence of survival (Webb and Peart 1999; Harms *et al.* 2000): the stronger drop in overall plant density where abundance was high, the rise in distance of survivors to adults, and the greater failure of seedlings in clusters of overlapping canopies. Mortality at Mount Remarkable was highest on the site and quadrats with greatest abundance of both adults and seedlings. Initially, some quadrats carried very diverse densities of seedlings, but at the end of two years, mortality had reduced the seedling population severely, and the remaining seedlings were much more evenly distributed over the site. This change in pattern demonstrates a very effective self-thinning process leading towards a density comparable to that of adults. The eventual growth pattern is further explained by processes captured by the other two spatial measurements.

As the approximately 20 % rise in the mean distance of survivors at Mount Remarkable over two years demonstrates, close proximity to the rapidly growing, resprouting adults had a negative effect on seedling survival. This effect is likely to result from direct competition for resources, especially water (Tyler and D' Antonio 1995) and light (Nagamatsu *et al.* 2002). While competition for resources is not universally accepted as a reason for seedling mortality, in this study, the enormous early growth with formation of multistemmed, leafy canopies by the *L.saxatilis* resprouts cannot be ignored as a detrimental factor in the ability of the much smaller seedlings to access soil resources and light, especially where adults themselves were placed densely (see Fig 3-10). Transfer of soil pathogens (Packer and Clay 2000; Bever 2003) or other diseases from adults, which themselves showed a drop in vigour, was also a likely cause of mortality (Webb and Peart 1999). The seedling population responded, therefore, as predicted by the Janzen-Connell hypothesis.

The majority of young seedlings emerged in groups with overlapping canopy. Clustering of seedlings may be due to unclear seed dispersal mechanisms or, as it can be speculated, through simple funnelling of seed by gravity and rain along the rocky, uneven surface structure into those pockets of soil which also collect and absorb rainwater and various surface particles, and due to this gathering of resources, represent suitable sites for growth. Accumulation of seed in these resource rich, “soft” spots may have resulted in the eventual emergence of seedlings in dense groups. However, the proportion of seedlings growing in groups dropped sharply after the summer 2012/13, and more so than expected from the overall high death rate. That grouping of seedlings is detrimental to their survival has also been found in other studies (Tyler and D' Antonio 1995; Webb and Peart 1999); this negative effect is to a great part again due to competition, especially for light and moisture, leading to dominance of larger seedlings over the smaller ones which perish (Weiner 1990), and also due to higher prevalence of disease (Fig 3-17) in clustered seedlings (Clark and Clark 1985). Altogether, the stress factors seedlings are subjected to are enhanced in interaction with each other (Ladd and Facelli 2005), with water availability ultimately being critical (Tyler and D' Antonio 1995; Gilbert *et al.* 2001). Together, they formed a strong selection force towards elimination of most seedlings emerging after fire, except for only a few which are the strongest, best adapted and best positioned.

### 3.5.5 Observed responses and known conceptual models

The observed variation in regrowth behaviour is possibly driven by the presence of different ecotypes of *L. saxatilis* or more likely, by external factors such as weather, season, phenological status and plant community with effects on fuel availability; this variation means that the dominant strategies of either seedling or sprouting are site- or population-specific rather than species-specific (Whelan *et al.* 2002). As a result, the species follows variable pathways within conventional models, as explained below.

**Fig 3-17 Diseased *L. saxatilis* seedling at Mount Remarkable in winter 2012**

Overall, *L. saxatilis* is a facultative resprouter with episodic recruitment particularly following fire; in absence of fire, seedling density is variable, but generally much lower. The pattern of emergence suggests that seed is predominantly dispersed locally near adults, and probably forms a persistent soil seed bank. The variability in regrowth pathways suggests that *L. saxatilis* follows several response types within conventional conceptual models. Within Grime's CSR model, *L. saxatilis* resprouts and regrows rapidly in a very competitive manner as type C, depleting resources and eventually showing signs of exhaustion; it recruits and given suitable conditions, matures rapidly after disturbance in the manner of a ruderal R. Finally, in the undisturbed habitat adults have the moderate growth rate and drought perseverance of a stress tolerator S (Grime 1977). Responses can follow the pattern of obligate seeders, such as observed after death of adults at Telowie, but resprouting from a woody base can also be very successful, as seen at Mount Remarkable (Noble *et al.* 1980); similarly put into Gill's terms, full leaf scorch at Telowie led to death and population recovery from soil stored seed, but at Mount Remarkable to resprouting from basal stems (Gill 1981). The species follows the pattern of Whelan's type D response at Telowie and type E at Mt Remarkable (Whelan 1995). In conclusion, conventional models do not well explain the range of regrowth and recruitment pathways of *L. saxatilis,* if applied on a species level, as their variation between sites is too great; but they serve well to explain the behaviour of individual populations.

## *3.6 Brief summary and conclusion of the field study*

Recruitment and growth pattern of *L. saxatilis* after fire can include resprouting as well as seedling recruitment. Recruitment appears to be strongly promoted by intermittent fires, so fire may aid long-term population persistence; it possibly assists the species in expanding its range. Resprouting is inconsistent; the recorded variation in growth patterns may point towards two different ecotypes, but a range of unmeasured, external factors are likely to be involved, probably ultimately leading to different fire severity, as expressed in the mortality rate of adults. Post-fire seedling survival patterns of this shrub are negatively density driven. Dependence on fire-free intervals and sufficient rainfall during the primary juvenile period of seedlings means that the species is potentially threatened by changes in fire regimes as they may occur under human management as well as those expected by climate change.

**Fig 3-18** ***L. saxatilis*** **in bloom at Mount Remarkable in September 2011**

# 4 *In-vitro germination of Logania saxatilis*

## 4.1 *Abstract*

Fire and other disturbances trigger germination of many plant species in Mediterranean-type habitats. Populations of the Rock Logania (*Logania saxatilis* G. Perry ex B. J. Conn: Loganiaceae), a rare native shrub of South Australia, had shown abundant seedling emergence after prescribed burning in the Southern Flinders Ranges. To determine the factors driving this recruitment event, five physical and chemical treatments (heat, light, smoke-water, nitrate and cold stratification) were applied to seed and germination was monitored over eight weeks. Smoke water had the strongest positive effect of any single treatment, leading to 58% germination in otherwise mostly dormant seed; light and nitrate also increased germination. The application of all treatments led to full germination. The synergistic effect of heat and nitrate on seed germination was found for the first time in a woody perennial of Southern Australia. It is concluded that germination requirements of *L. saxatilis* are typical of a colonising species with strong recruitment after fires, but he species also responds to other disturbance events that destroy aboveground biomass or disturb soil. Adequate fire management may be essential to sustain populations of this rare species.

## 4.2 *Introduction*

Disturbance in established plant communities benefits germination and seedling recruitment of many plant species (Grime 1973). The specific changes to the environment associated with disturbance can signal increased resource availability (e.g. nitrates, light) and absence of competition (e.g. light, soil temperature) to neighbouring plants or seeds (Sousa 1984). Small disturbances offer a gap for regeneration in an otherwise unchanged vegetation community. Disturbances of a larger scale may be caused by extensive vegetation loss, for example after severe storms or drought (Benwell 2007), or by fire, a common disturbance in Mediterranean-type habitats worldwide (Staden *et al.* 2000). Compared to other disturbances, fire has additional and very specific physical, chemical and environmental effects. Some species germinate and emerge in response to heat and smoke which activate dormant seed stored on the plant itself or in a soil seed bank (Keeley and Fotheringham 2000). However, observations of fire response in the field cannot ascertain whether post-fire recruitment has occurred specifically in response to fire, or as a result of the generally increased availability of resources such as space, light and nutrients.

In contrast to field monitoring, *in vitro* germination experiments allow the application of fire-specific seed treatments separately from those representing generic disturbances. We investigated the specific factors that may trigger germination of *L. saxatilis* seed, by applying four physical and chemical clues mimicking fire (dry heat, smoke-water) and generic disturbance (nitrate and light). To assess the possible impact of temperature changes on germination behaviour, as well as a potential requirement to undergo cold conditions to germinate in spring only, cold stratification of seed was also included as a fifth treatment. With this experiment, I sought to understand germination requirements of *L. saxatilis,* with a view towards contributing to the development of successful management practices for this rare species.

## 4.3 Methods

Seed of *L. saxatilis* was collected in December 2010 at the Mount Remarkable Range, Southern Flinders Ranges, from ten plants within a subpopulation of about 30, about two years prior to the experiment. Fruit capsules were dry, split open at the top and of dark brown to black colour at the time of picking. Seed was separated from most associated debris such as capsule material by sifting and then stored in brown paper bags for two years under dry conditions at room temperature which fluctuated with daytime and seasonal changes. Seeds of typical size and appearance for the population (dark brown, about 1.5 mm long, ovate, and somewhat flattened with a concave and convex surface each, see Fig 4-4) were subjected to a viability test by cutting four replicates of 25 seeds lengthwise under a microscope. This usually revealed a structure presumed to be a large embryo surrounded by endosperm. Based on the integrity of these structures, the viability of the seed was estimated to be 96 % (Fig 4-5).

The five treatments (heat H, smoke S, nitrate N, cold moist stratification F, light regime light L or darkness D) at two levels, present or absent, in all combinations (orthogonal design), resulted in 32 different treatments and with four replicates, in 128 independent experimental units overall, as illustrated in Fig 4-9. Lots of 25 seeds stored in test tubes were allocated randomly to treatments. All treatments were applied to the replicates independently, thereby avoiding pseudoreplication (Morrison and Morris 2000). A temperature of 80°C (Kenny 2000; Steggles 2012) was applied as a 15 min pulse treatment in an oven; it was monitored with a sensor inserted into a centrally located test tube and connected to a digital thermometer outside the oven (Fluke 52). Boiled reverse osmosis (RO) water stored in a sterilised glass jar formed the basis of all treatments and irrigation (when required to maintain hydration of the seeds) during the eight weeks of incubation. Smoke exposure was simulated by immersion of seed in 1 ml of a 10 % solution of the commercial product Smokemaster-R (Vigilante *et al.* 1998) for 24 h, followed by a single rinse with 1 ml RO water and drying at room temperature, while controls were soaked in RO water for the same time. During cold stratification seed was stored with 0.2 ml RO water for two weeks in a cold room at 5°C. The nitrate solution of 100 $mg^{-l}$ $KNO_3$ solution was individually prepared for each replicate and 1.5 ml applied at the beginning of incubation as a chronic treatment, after transferring seed from the test tubes to 50 mm petri dishes with four layers of filter paper (Filtech 55 mm equivalent to Whatman Grade 1, Fig 4-8). Controls received pure RO water. Light exclusion was achieved by wrapping the dishes in aluminium foil. General hygiene practices were followed to avoid establishment of mould or other infection. Petri dishes, in stacks of four, mixed across the replicates and all treatments as far as possible, were sealed in a double layer of plastic wrap to reduce evaporation. However, smoke treated seeds formed separate stacks, as they emitted a distinct smoke scent, indicating the possible risk of cross-contamination of controls. Treatment combinations involving cold wet stratification took an additional two weeks to complete and for this reason, formed their own two batches, but were eventually incubated together with the above earlier lot. Petri dishes were rotated within the stack each time they were handled (once to twice a week), and were also exchanged between stacks at the time of counting (once a week).

Incubation with broad spectrum light at a daytime length of 12 h at 24°C and 18°C at night was chosen to reflect the spring and early summer conditions in the Southern Flinders Ranges; field observations suggest this to be the time of natural germination. Germination was defined as the protrusion of the radicle through the cracked shell of the seed as in Fig 4-6 and Fig 4-7. Germinating seeds were counted and removed first on day eight of incubation in light, and then at weekly intervals for a further seven weeks; seeds received RO water as needed after each count. Dark treatments were counted with green light, produced by covering a light source with four layers of coloured cellophane; they were not counted until week two, in order to minimise exposure to light during the early processes of treatment response.

By measuring germination on a weekly basis, not only the overall effect of treatments on the final rate was captured, but also their capacity to accelerate germination during incubation. This was considered important, as it may indicate earlier emergence of seedlings under natural conditions. Germination counts after week one, after week two, cumulative to end of week two, and cumulative to the end of week eight represented all observed effects well, and they formed the basis of the analyses. Analyses were performed using JMP IN 4 version 4.0.3 with multifactorial ANOVA. Unequal variances resulted from data being bounded by the maximum germination of all 25 seeds, leading to clustering of data where germination rates were high. We reduced this heterogeneity with square root and $\log_{10}$ transformations. Post-hoc tests with Dunnett's method were applied to investigate interactions and comparisons between germination rates were also drawn using the method of (Kenny 2000).

## *4.4 Results*

Germination started in the first week and reached its peak by the end of the second; little change occurred after the fourth, and by eight weeks germination had practically ceased (five new seedlings across all 128 petri dishes between weeks six and eight). Germination was observed in all single and combined treatments, but differences in germination rates were significant (Fig 4-1), the final counts at eight weeks averaging from 11 % to 96 %.

### *4.4.1 Germination rates*

Above all, the effect of smoke-water was highly significant (Table 4-1) and of all treatments it had the strongest positive impact on germination (Fig 4-2), demonstrated by its contribution of 70 % to the total sum of squares (Table 4-1). All treatment combinations that involved smoke-water resulted in a higher final germination rate (mean 82.1 %) than their controls without smoke (mean 33.9 %, Fig 4-2). Smoke-water by itself was effective in raising germination rates as much as the most efficient treatment not involving smoke, which was the combination of heat, nitrate and light; either led to a final germination of 58 % (Fig 4-1); all other treatments involving smoke-water led to higher final rates than this and all other treatments not involving smoke-water to a lower rate. Importantly, the combination of all treatments led to the overall strongest germination of 96 % (Fig 4-1), which is the same as the viability rate, representing full germination.

The effect of light was highly significant (Table 4-1) and after smoke-water, it had the second strongest positive impact on germination, although its contribution of 4.5 % to the total sum of squares reveals a much weaker effect than the above. Without any other treatment, 37 % of seed germinated in light and 19 % in darkness. Light was effective without other factors, but it also had a further positive, additive effect to other treatments (Fig 4-1). Incubation in light resulted in more successful germination than incubation in darkness in 31 of the 32 treatment combinations (mean rate of germination with light was 64 % versus 51 % without light, Fig 4-2).

Heat not followed by incubation with nitrate had no effect on germination rates (Table 4-1, Fig 4-2). However, in combination with nitrate a distinct positive effect on germination rates was found.

The effect of nitrate was highly significant (Table 4-1) and after smoke-water and light, it had the third strongest positive effect on germination. The average germination rate across all treatments involving nitrate (but not heat) was 61 % versus 50 % in controls (Fig 4-2). Those treatments involving nitrate, as well as heat, were subject to a synergistic interaction between the two factors; this interaction further increased germination rates to an average of 70 % versus 52 % in controls (Fig 4-3). Seeds subject to heat, nitrate and light had the highest germination rates of seed not treated with smoke (Fig 4-1).

The effect of cold stratification was also significant (Table 4-1), leading to an overall slightly lower final germination rate than in controls (difference of 4.4 %).

**Table 4-1 Effect of treatment factors on final seed germination**

| Effect | p | SS | F-ratio | % of Total SS |
|---|---|---|---|---|
| Smoke | <0.001 | 5164 | 515.17 | 70 |
| Light | <0.001 | 335 | 33.4 | 4.5 |
| Cold stratification | 0.0226 | 54 | 5.37 | 0.7 |
| Heat | 0.1148 | 25.38 | 2.53 | 0.3 |
| Nitrate | <0.001 | 549 | 54.7 | 8.4 |

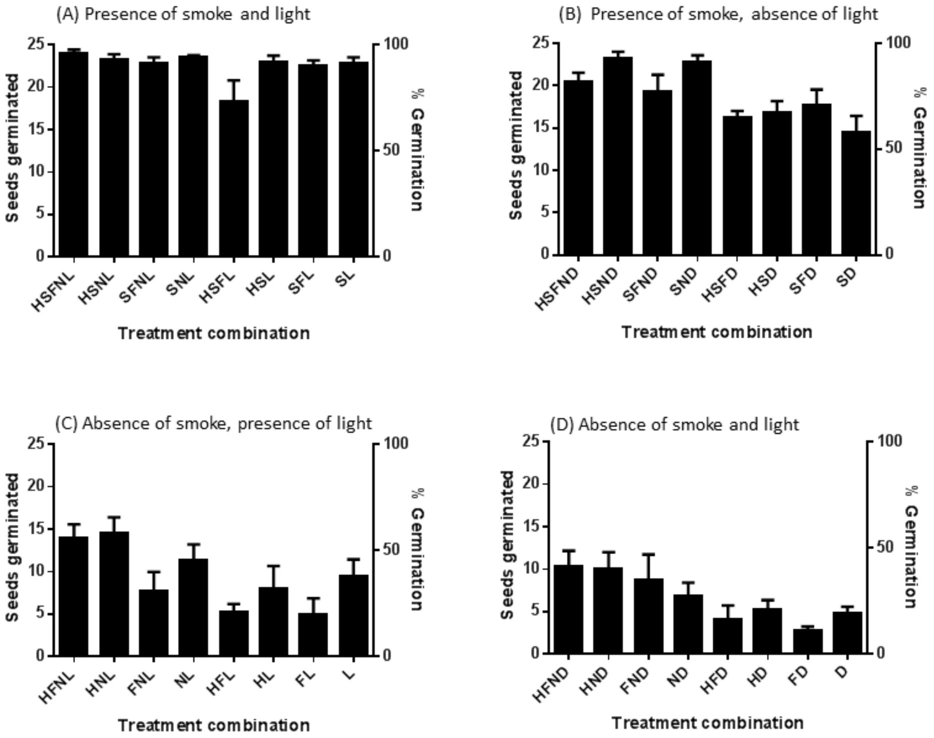


**Fig 4-1 (A)-(D) Germination results as means and SEM of the four replicates of all 32 treatment combinations, using 25 seeds each. Results are sorted in four groups according to presence of absence of the two strongest positive triggers of germination, which were smoke-water (S) and light (L). Heat (H) and nitrate (N) acted synergistically to raise germination. Cold stratification (F) mostly reduced germination rates. Absence of (L) as darkness (D) also reduced germination.**

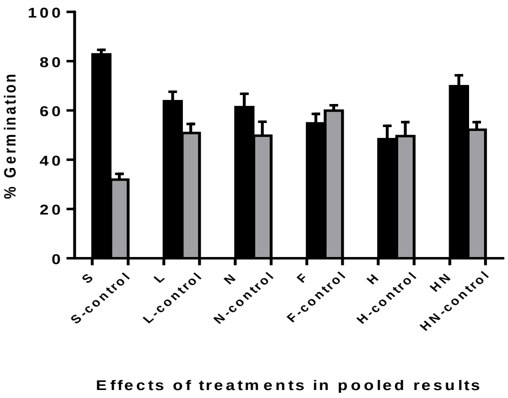


**Fig 4-2 Mean and standard error (SEM) of the 16 treatment combinations of each factor versus mean and SEM of the 16 others (-control), displayed as germination rate (100% equivalent to germination of all 25 seeds). Treatments (black) are smoke (S), cold stratification (F), nitrate (N), light (L), heat (H). Controls (grey) include all other treatments.**

### 4.4.2 Germination speed

Germination speed varied across treatments, as found in the early seed counts after one and two weeks of incubation (Fig 4-3, Table 4-2). In particular, seed treated with smoke and nitrate as well as with smoke and light germinated faster. Some of the findings regarding germination speed are ecologically relevant as they may lead to earlier emergence of seedlings in the field, allowing a longer growth season for establishment; such is the faster germination of seed as a result of interactions between smoke and light, and between smoke and nitrate (in seeds not heat treated). Faster germination was also observed in seed treated with cold stratification, but this is considered an artefact as a result of (cold-) enforced quiescence after dormancy had already been released through smoke treatment, and not considered ecologically relevant (see Discussion).

**Table 4-2 Effect of interactions between treatments as observed by seed counts after weeks one and two**

| Effect | Incubation interval | p | SS | F-ratio | % of Total SS | Ecological relevance |
|---|---|---|---|---|---|---|
| Smoke x nitrate | Week 2 | 0.0113 | 54 | 6.94 | 2.4 | yes |
| Heat x nitrate | Week 2 | 0.0142 | 51 | 6.48 | 2.3 | yes |
| Smoke x light | Week 1&2 | 0.0465 | 43 | 4.07 | 7.2 | yes |
| Smoke x cold stratification x nitrate | Week 1 | 0.0291 | 23 | 5.06 | 2.7 | no |
| Smoke x cold stratification | Week 2 | 0.0113 | 54 | 6.93 | 2.4 | no |
| Smoke x cold stratification x nitrate | Week 2 | 0.088 | 24 | 3.032 | 1.1 | no |

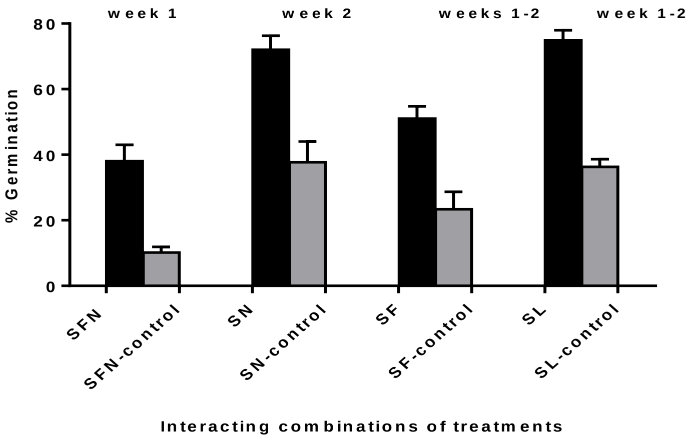


**Fig 4-3 Pooled data of germination counts at one and two weeks after start of incubation showing certain combinations of treatments that increased germination through interactions at this point in time. Interacting treatments (black) are smoke (S), cold stratification (F), nitrate (N), light (L), heat (H). Controls (grey) include all treatments not involving a combination of the interacting factors.**

## *4.5 Discussion*

### *4.5.1 General considerations*

The germination rate of untreated two year old seed was less than 20 %, but the application of treatments mimicking fire and other types of disturbance resulted in much higher germination rates. The link between treatments and germination rates points towards the presence of physiological dormancy, which after two years of storage may be primary (developed during seed maturation on mother plant), or secondary (seed has acquired dormancy) (Hilhorst 1995). More detailed study of the seed is necessary to determine the type of dormancy with certainty, but extrapolating to the natural habitat of *L. saxatilis*, the findings strongly suggest that in unburnt habitat a large proportion of seed is retained in a persistent seed bank, as in other South Australian vegetation communities (Rawson *et al.* 2013), and as generally in woody species that grow in habitats subject to intermittent fire (Keeley 1987; Grime 2001).

**Fig 4-4 Seed of *L. saxatilis***

Seed is activated to varying degrees when the environment is favourable for plant establishment (Lambers *et al.* 2008), such as after certain disturbance events, above all fire. Apparently the post-fire environment represents an ideal recruitment opportunity for this species, and with suitable light and moisture the response is rapid: Germination of *L. saxatilis* was faster than in reports for other species of *Logania* (33 days for *L. vaginalis*, 72 for *L. buxifolia* (Fryer 2006); experimental details not known) and also faster than many other species subjected to seed germination treatments (Hidayati *et al.* 2001; Kenny 2003; Olmez *et al.* 2006; Olmez *et al.* 2007; Hidayati *et al.* 2012).

### 4.5.2 Role of the response to smoke

Exposure to smoke-water was the strongest single trigger of germination in two year old seed. That smoke overcomes dormancy is now a well-demonstrated phenomenon for flora in Australia (Lloyd *et al.* 2000) and elsewhere (Lange and Boucher 1990; Keeley and Fotheringham 1998; Crosti *et al.* 2006). Synergistic interactions of smoke with other factors, as in the high initial germination rate of *L. saxatilis*, have also been demonstrated by a number of other studies. For example, interactions with heat (Gilmour *et al.* 2000; Kenny 2000; Tieu *et al.* 2001; Thomas *et al.* 2003), light (Keeley and Fotheringham 1998), cold stratification (Tsuyuzaki and Miyoshi 2009), and soil burial (Turner *et al.* 2009) are known.

**Fig 4-5 Cut seed of *L. saxatilis* for visual assessment of viability (right seed**

The smoke-water effect provides an important insight into the recruitment strategy of the species, and it contributes substantially to an explanation why fire in the habitat of *L. saxatilis* triggered a major germination event, as recorded in the field study. Firstly, the smoke effect alone could lead to about 58% activation of buried seed, and given that karrikins are water soluble (Nelson *et al.* 2012), they can be expected to travel into the soil profile to some degree and affect more deeply-buried seed. Secondly, where fire intensity is sufficient to lead to extensive vegetation death with consequent increased light influx and nitrate availability (in addition to the smoke effect), virtually all seed affected could be expected to respond. Thirdly, sediment movement occurs after fire on steep slopes (Morris *et al.* 2013), such as those favoured by Rock Logania, could assist further in secondary seed movement to the surface, exposing even more seed to the above influences, resulting in further activation of the soil seed bank, and in the rapid response of seed under the impact of smoke and light combined.

The implications of this observed powerful reaction to smoke are diverse. For example, it could lead to reestablishment or expansion of the population and given the strong response of the species to fire, recruitment in the post-fire environment is clearly a key strategy of this species (Bell 1999). However, it also reveals a potential vulnerability: extensive germination may leave the seed reserves close to depleted (Noble and Slatyer 1980; Auld and Denham 2006). As a consequence, further recruitment may not be possible before new seed has been produced ,or dispersed into the site, and population survival may then depend entirely on successful maturation of the young recruits (Burrows 2013b), or the ability of adults to resprout after fire (Bond and Midgley 2001).

Where population recovery after a fire relies on successful seedling recruitment alone, these seedlings would need to reach maturity to rebuild the seedbank. This means that *L. saxatilis* is potentially highly sensitive to catastrophic events during this period of establishment. Such events could be two or more fires in close succession, or other detrimental events following an initial fire, such as recurrent disturbances or severe drought, which after the established adults have already been lost, could reduce or annihilate the seedling cohort emerging in the following seasons. Only once recruits or resprouts have attained maturity can resilience to any potential new major disturbance be restored, be it fire or otherwise (Auld and Denham 2006).

**Fig 4-6 Germinating seed of *L. saxatilis* during germination test**

### 4.5.3 *Role of the response to light*

Broad spectrum light in a regime of equal day and night length increased germination through releasing dormancy; this is observed frequently in small-seeded species that are responsive to disturbance (Pons 2000) and in species from Mediterranean ecosystems (Luna and Moreno 2009). However, as testing the effect of different spectra of light was not included in the experiment, differentiation between potential effects of canopy shade versus complete darkness is not possible (Mendoza-Hernández *et al.* 2010), but general conclusions can still be drawn. As shown for *L. saxatilis*, parallel responses to other treatments also indicating disturbance, such as nitrate (Hilhorst and Karssen 2000) are common findings, as well as fire response (Luna and Moreno 2009).

Prior heat treatment may render seed more susceptible to light (Pons 2000), but this was not the case in *L. saxatilis*. Light response may also vary with incubation temperature (Vincent and Roberts 1977). Duration of exposure is also known to be relevant (Pons 2000) and amongst related genera, a light response has been demonstrated for *Mitrasacme* and *Buddleja* (Vàzquez-Yanes and Orozco-Segovia 1990).

Positive photoblastic response ensures that germination only takes place, when soil cover is shallow enough for the emerging small embryo to reach the surface and commence growth (Pons 2000). To reach this position, seed must either be dispersed directly from the mother plant to the surface, or already dispersed seed in the soil seed bank must be disturbed, releasing it from deep burial (Hilhorst and Karssen 2000; Alboresi *et al.* 2005; Luna and Moreno 2009). Such disturbance often also helps to remove competing established vegetation (Bell *et al.* 1999), further increasing the chance of successful seedling establishment and growth. Without disturbance, many seeds remain dormant buried in the soil or located under dense vegetation, awaiting a suitable recruitment opportunity. Disturbance leading to sudden availability of light, or secondary dispersal of seed to the soil surface may be provided by removal of litter and/or ground-covering vegetation, animal activity, rock movement, the appearance of a canopy gap, or other forms of soil erosion (Pons 2000); all of these processes are observed commonly on the steep slopes in the habitat of *L. saxatilis.*

The relatively low germination rate resulting from light exposure alone may represent an adaptation to the low overall chance of recruitment success, as disturbance may be very limited spatially, as was also seen for nitrate (see below). However, a much increased germination effort was seen where exposure to light was combined with other disturbances such as smoke and nitrate, suggesting the evolution of multi-trigger recruitment responses that require disturbance combinations to optimize conditions for seedling growth.

### 4.5.4 *Role of the response to nitrate*

The presence of nitrate had, after smoke and light, the third strongest effect on germination. Nitrate boosted germination in some studies (Hilhorst 1990; Thanos and Rundel 1995; Bell *et al.* 1999; Alboresi *et al.* 2005), but not others (Steggles 2012). Nitrate response has often been linked to light (Keeley and Fotheringham 1998; Bell 1999; Hilhorst and Karssen 2000; Luna and Moreno 2009), and it has been suggested that nitrate binds to a phytochrome receptor on the cell membrane, which is then activated by phytochrome far-red formed under the influence of light (Pons 2000); this process would require light also to be present for a nitrate effect. However, a dependence on light was not found in *L. saxatilis*, where both treatments acted independently from each other (see below). An involvement of nitrate with gibberellic acid or abscisic acid has also been suggested (Alboresi *et al.* 2005), and a response to nitrate has been known for a long time for some species with the potential to be crop weeds (Steinbauer 1957). As for light, nitrate availability is also clearly linked to various disturbances with or without fire (see below).

A significant interaction raising final germination rates was evident in seed treated with 80°C heat followed by incubation with nitrate. Interactions involving nitrate have been reported in other studies, interactions with light being the most common (Toole *et al.* 1955; Goudey *et al.* 1988; Hilhorst 1990; Keeley and Fotheringham 1998; Bell 1999; Hilhorst and Karssen 2000; Luna and Moreno 2009). Interactions with light regime and cold stratification (Thanos and Rundel 1995) as well as with incubation temperature (Toole *et al.* 1955; Bian *et al.* 2013) have also been reported. The interaction between heat and nitrate is not a common finding; only in a tropical herbaceous legume, an interaction between nitrate and 80°C heat was demonstrated by (Williams *et al.* 2003) and interpreted as a mechanism to ensure quick development of the ephemeral after fire; for a woody species of Southern Australia this interaction has not been previously reported, and the mechanism of the effect is unclear – it seems that heat rendered seed more susceptible to the effect of nitrate. It offers an interesting avenue for further investigation.

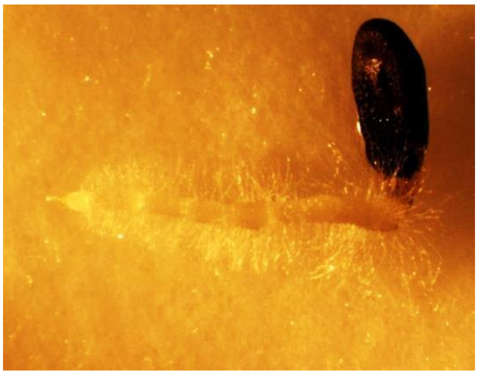


**Fig 4-7 Growth of root in germinating *L. saxatilis***

Nitrate represents a very important nutrient for growth; a dependency of germination on nitrate availability encourages recruitment when nutrients levels in the seed environment can support growth (Alboresi *et al.* 2005). The nitrate requirement of the species for successful establishment may be particularly high, and germination may have evolved to occur selectively in a high nitrate environment. The observed germination rate under the impact of nitrate is moderate, so events raising nitrate levels alone would only activate a limited proportion of the seedbank. This is an advantageous strategy, as it matches the recruitment success: in contrast to the processes during a fire event, the extent of these disturbances is not necessarily profound enough to allow new plant establishment. Surviving root systems of the damaged plants, growth of established neighbours, or an active population of herbivores may interfere with newly emerging *L. saxatilis* seedlings and prevent their successful growth. Therefore, while the chance of successful recruitment after a single such disturbance is small, the moderate germination rate ensures that much seed is retained in the seedbank. As for the light response, this means that recruitment can be attempted repeatedly whenever these minor disturbance events occur; failure of seedlings after some of these events is not catastrophic. This strategy of bet-hedging is well documented for other plants in hostile

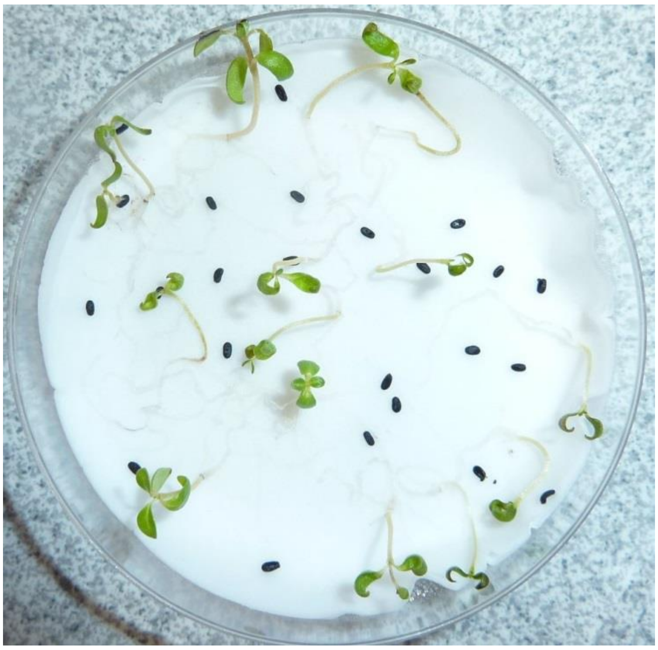


**Fig 4-8 *L. saxatilis* during germination test. Germinating seeds were usually removed during counts but remained in this dish for photography**

environments (Philippi 1993). Nitrate soil content can also rise after fire, and in this context, the nitrate response represents an adaptation to fire.

### *4.5.5 Role of the response to the combination of heat and nitrate*

In a natural habitat, the sequence of heat and nitrate can easily be related to the passage of a fire followed by soil processes leading to nitrification. However, extreme summer temperatures in the semi-arid, open rocky habitat, followed initially by vegetation death and then rainfall, or change of season, may also result in this combination of impacts. Hence, the interactive effect of heat and nitrate is not fire specific, but could be promoted by fire. As by light and nitrate, the extent of disturbance and opportunities for establishment are not transmitted by nitrate alone, and as only a part of affected seed responds, repeated disturbance can be tolerated, and it will probably lead to repeated attempts at recruitment, to be eventually successful. Resilience of the population is maintained under the same conditions as for the light and nitrate response.

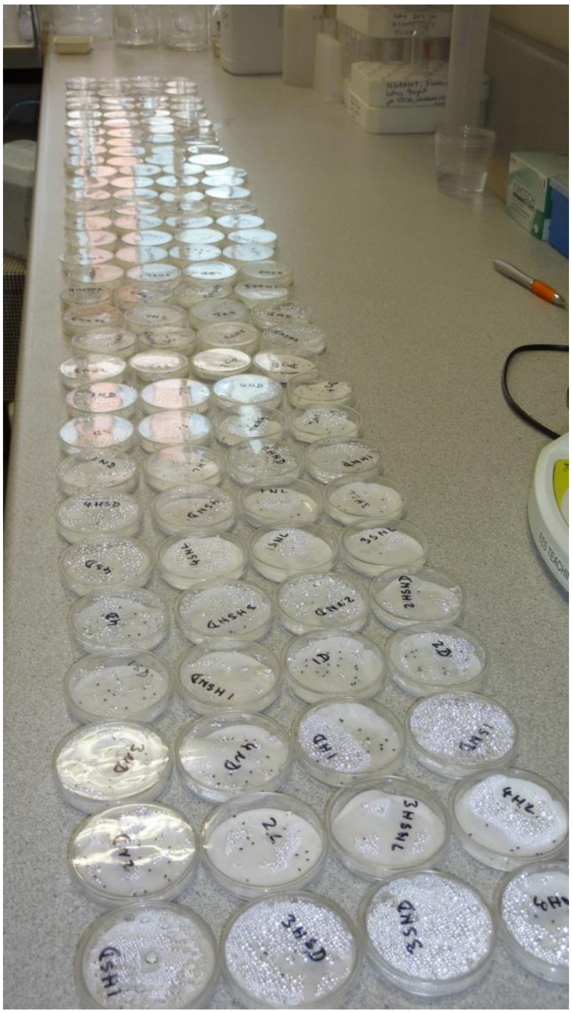


**Fig 4-9 All petri dishes unwrapped and lined up at the conclusion of the experiment!**

### *4.5.6 Role of the response to cold stratification*

The conclusions that can be drawn from cold stratification in this experiment are moderated by the fact that it involved a delay of two weeks after smoke treatment, and without further experimentation the effect of this delay cannot be separated from the effect of the cold itself. Consequently, the conclusions are tentative. Cold treatment had diverse and sometimes apparently opposite impacts on germination rate. On average, cold stratification lowered the final germination rate in *L. saxatilis.* This effect was quite marked where the treatment was applied without any others (Fig 4-1). Comparison with other studies shows variability in responses of different species; both weakened (Hilhorst 1990; Shahi-Gharahlar *et al.* 2012) and enhanced (Ali *et al.* 2010) overall germination success after cold stratification have been reported, and dependence on length of stratification period (Olmez *et al.* 2006; Olmez *et al.* 2007), and temperature regimes is also known (Hidayati *et al.* 2001). The reason for a potential germination response when incubating seed after cold stratification lies in a signal effect (Toole *et al.* 1955). Possibly pre-chilling promoted the effect of the other seed treatments (Vincent and Roberts 1977): in *L. saxatilis*, germination was rapid in seed treated with the combination of smoke-water, nitrate, and cold stratification. However, the reason the fast germination after chilling is probably that cold conditions initially forced the seed into quiescence (Baskin and Baskin 2004), but actual dormancy was released due to the prior treatments, for example with smoke-water; and once the seed was returned to warm conditions, the radicle emerged rapidly. This means that the effect of apparently fast germination is probably an artefact of the experimental conditions.

As a result, the effect is of interest in the context of seed physiology, rather than the plant's ecology. Cold stratification was not a prerequisite to germination, so seed in the natural habitat does not have to undergo winter conditions that may involve temperatures of 5°C; the response does not allow the conclusion of a preference for spring germination. This interpretation is in accordance with Bell *et al.* (1993), who expressed doubts that a response to seed chilling would offer an ecological advantage to Mediterranean flora, and according to ten Brink *et al.* (2013) at least some species with a preference for open habitat lack a response. The effect has no ecological significance, other than suggesting a limited tolerance of very cold conditions, possibly because the natural habitat of *L. saxatilis* in the Southern Flinders Ranges, where the seed was sourced, is not likely to experience long periods of such low temperatures.

### *4.5.7 Role of the response to heat*

Heating the seeds to 80°C for 15 minutes without adding nitrate to incubation did not affect final germination rates. The finding agrees with reports by Keeley and Fotheringham (2000) that heat is not necessarily a stimulating factor in germination even in species showing strong recruitment after fire. However, a wide range of temperatures from about 50°C (Thomas *et al.* 2003) to 120°C (Tieu *et al.* 2001) have been used successfully for different species in germination experiments, so a different temperature than 80°C would perhaps result in a detectable response in *L. saxatilis*.

## *4.6 Brief summary and conclusion of the germination experiment*

The findings of the germination experiment explain processes behind the observed strong recruitment in the field after fire, which is predominantly triggered by smoke in combination with availability of light and nutrients such as nitrate. Fire is a key recruitment opportunity for *L. saxatilis,* as demonstrated by the strong response to smoke-water, and high germination rates can be expected after prescribed burning. However, this will also draw strongly from the soil seedbank, limiting the response capacity to a second fire in short succession. Sufficient time for maturation of regrowth and reestablishment of the soil seed bank is a critical aspect of post-fire recovery. The species may be very sensitive to high fire frequency, and fire management decisions need to take into account the risk and frequency of naturally occurring fires in addition to prescribed fires. Germination is also triggered by other forms of disturbance which increase influx of light and nutrients on seed, and are likely to lead to gap recruitment under favourable conditions.

# 5 General conclusion

This study investigated the role of fire in the persistence and recruitment of the rare shrub *L. saxatilis* in the Southern Flinders Ranges. The combination of monitoring post-fire regrowth in the field with a laboratory-based test of the germination requirements led to some important insights into the recruitment strategy of the species. The results highlight the important role of fire in the vegetation of the Southern Flinders, outline potential threats to the persistence of its now fragmented, fire-driven flora, and offer some contributions to its management.

## 5.1 Experiments summary

Two experiments, a field study in the Southern Flinders Ranges, and a laboratory-based germination test, investigated the recruitment and growth of *L. saxatilis* in response to fire. The field study involved pre- and post-fire monitoring across two parks, Mount Remarkable National Park and Telowie Gorge Conservation Park (Fig 5-1, Fig 5-4). The germination study tested the response of seed collected at Mount Remarkable to various triggers, either related to general disturbance, or exclusively to fire. In all experiments, fire emerged as the strongest driver driver of recruitment. Some variation in regrowth strategies was apparent between the two parks, as resprouting was inconsistent, and recruitment in the absence of fire was also variable.

Without the involvement of two separate locations into the field study, this width of responses would not have been recorded. It is concluded that spatial and temporal heterogeneity must be taken into account when assessing the response of plant species to disturbance regimes, as also found by other researchers (Benwell 1998).

**Fig 5-1 Site MB2 at Mount Remarkable about 10 months after burning**

Density-dependent effects on seedlings eventually led to a pattern of evenly spaced recruits on burnt sites. Intense early intraspecific competition for moisture, light and nutrients such as nitrate of resprouting adults (where still present) with seedlings and amongst seedlings imposed strong selection forces on the initially numerous and typically clustered recruits. This selection was further driven by disease in winter and high moisture stress in summer. Positioning of seedlings in relation to each other and to conspecific adults had a strong influence on survival, as resprouting adults reduced the establishment success of nearby seedlings. Only a small percentage of the best adapted, most vigorous and suitably positioned seedlings survived to the end of the study period.

The response of seed to *in vitro* treatment with physical and chemical cues related to fire underlined the adaptation of the species to fire, as smoke water triggered the greatest germination rate of all single treatments, and led to full germination when combined with other cues such as light and nitrate. This additive effect of several treatments highlights the relevance of fire in clearing and preparing habitat, and demonstrates the species' ability to perceive these habitat changes, in order to take full advantage of the resource availability following fire (Fig 5-3).

## 5.2 The role of fire in recruitment

The strong positive impact of fire on germination reveals a specific adaptation of *L. saxatilis* to the intermittent exposure to natural wildfires (Gill 1981). This adaptation points towards poor success of young individuals in undisturbed habitat, as it was observed at Mount Remarkable. Fire probably assists the species in maintaining its range through temporary suppression of competing factors, allowing a time window for populations to rejuvenate through a surge of seedlings. Smoke as a unique property of fire has evolved to be the chemical trigger in the recognition of fire by seed of *L. saxatilis*. Smoke is the messenger, but it is the effect of fire itself, by clearing space and making nutrients available, that provides the conditions for successful establishment of young seedlings. As outlined above, fire appears to activate a very large proportion of available seed, probably stored in a persistent soil seed bank, and this seed can only be replaced by seed deposits from mature plants. Assuming that the entire population is affected by fire, these mature plants will either be resprouted survivors, or new recruits that take some time to grow to adulthood after fire. The dependence on the soil seed bank renders the species sensitive to high fire frequency, as the essential regrowth period may be interrupted by fires in quick succession.

Resprouting potential of *L. saxatilis* is probably linked to either intraspecific differences or exogenous factors that affect plant survival after fire; the enormous growth rate may be supported by plant and soil stored resources, which may be depleted immediately after regrowth, and until replaced, would render resprouting success threatened by a second fire in close succession, similar to the regrowth from germination. Both response forms depend on fire-free intervals for growth and seed production. On the other hand, absence of fire over very long periods of time may prevent recruitment in a competitive environment, and lead to gradual population decline. The current known fire frequency of about 23 years at Mount Remarkable has allowed for both the adult population to persist, and for sufficient recruitment to occur.

Given the adaptation of this species to burning, fire is clearly an integral part of the historic natural dynamics of vegetation in the landscape of the Southern Flinders Ranges. Fire briefly rearranges the competitive situation between different species and age groups to the advantage of *L. saxatilis* and similar species capable of responding with rapid regrowth, or strong germination. This also implies that for certain other species, fire must lead to an at least temporary disadvantage, and these species may require a fire regime different to that of *L. saxatilis*, such as for example longer fire free intervals. In conclusion, the response of species to fire in the same habitat must be heterogenous, and this must be considered when applying fire to reserves of the Southern Flinders Ranges.

**Fig 5-2 Historic fire scar, Southern Flinders Ranges**

## *5.3 Fire management*

In general, it seems that occasional fire is necessary for distinct, spatially broad recruitment events across the *L. saxatilis* populations. A fire interval of around 20 to 60 years, as currently provided by natural wildfires in the Southern Flinders Ranges, seems to allow for sufficient recruitment opportunities. Given the probable risks to the population associated with high fire frequency, prescribed burning is only indicated if and where it replaces wildfire. If this cannot be expected, and unplanned fires can follow prescribed burns at short intervals, prescribed burning may pose a threat to *L. saxatilis.* From the regeneration processes observed so far, it can be hypothesised that a fire frequency of 10-15 years represents the minimal fire interval. However the actual regeneration success leading to the reestablishment of an equivalent population will be determined by the pathways of regrowth, and by the quality of the post-fire environment, especially rainfall (Croft *et al.* 2010).

Being a facultative resprouter, *L. saxatilis* will either resprout and additionally germinate after fire, or be limited to germination alone after death of the pre-fire plants. This distinction is possibly related to fire severity. Resprouting accompanied by additional seedling emergence is the more fire-robust response as it involves population continuity. The obligate seeding response, when taking place without the presence of resprouting adults, carries a higher probability of successful recruitment of new plants, but is also carries an overall higher risk of failure and is the more fire-sensitive response type (Bradstock and Kenny 2003).

This diversity of potential responses apparently leaves a choice of either treating populations with low fire intensity to keep adults alive, and encourage some additional seedling growth, or have a higher intensity prescribed burn and remove much of the present vegetation, be it adult, senescent or otherwise, to provide the optimal conditions for seedling establishment. As higher fire intensity is connected to greater heat, fire front and often fire speed, the chosen method will have some bearing on the extent of the fire within and beyond the *L. saxatilis* population.

Patch burning, given its usually low fire intensity, can be expected to result in recovery of adults and some seedling emergence and recruitment, even if reduced by the ongoing presence of adults. Regrowth success could be furthered by burning after the recharge of soil moisture from rainfall. By burning only a small part of the population each time, this strategy can be applied repeatedly over several years, and effectively spread the establishment risks to seedlings over a number of growth seasons. In a landscape burn, potentially higher fire intensity and severity have to be taken into account when predicting the impact on *L. saxatilis*. In any such burn the loss of the adult population has to be expected, and the species may be limited to the response of an obligate seeder. Persistence of the population depends on maturation of seedlings, which in return require suitable conditions for successful growth.

Successful recruitment of obligate seeders is driven by benign conditions during the initial establishment period of seedlings which is at least the first year – even if mortality can still be very significant after this time, as study of *L. saxatilis* showed.

This risk of mortality and potential failure of reestablishment emphasizes the responsibility of fire managers to plan ahead, and take into account, the likelihood of sufficient rainfall over the season following the burn. In Southern Australia, some predictability of seasonal rainfall is given by El Niño/ La Niña events. It follows that where fire is applied for regeneration, particularly of rare flora such as *L. saxatilis*, prescribed burning should be timed in accordance with these predictions: dependence on regeneration from seedlings magnifies the extinction risk imposed on the isolated populations within a fragmented landscape, whenever fire affects their habitat.

## 5.4 Non-fire related aspects of recruitment

The presence of a variety of age sizes in habitat unburnt for 60 years at Telowie demonstrates the ability of this population to recruit without the direct exposure of its habitat to fire. This may be due to the presence of a different ecotype, or indirect effects of fire, such as possibly smoke drift from nearby burns, or entirely unrelated to fire, through other disturbance that lead to availability of light and nutrients and resulted in gap recruitment (Ooi *et al.* 2006). Recruitment without fire was less apparent at Mount Remarkable, but the response of seed from this population to non-fire related factors such as light and nitrate reveals its ability to recognise disturbance without fire. Typical minor disturbance events as they may occur in its steep rocky habitat (Fig 6-2), such as rock and soil movements and tree fall, can trigger gap recruitment through exposing dormant seed to light, and where applicable, increasing soil nutrient through decomposition of damaged plant material. Moderate animal browsing may have a similar effect by reducing the plant canopy over the soil surface, disturbing soil through movement and adding nutrients through droppings. These processes apparently allow for the successful gap recruitment of *L. saxatilis*.

**Fig 5-3 A study site at Mount Remarkable shortly after burning in autumn 2012**

However, ongoing heavy disturbance is likely to affect the seedbank through gradual exhaustion and interfere with successful growth and maturation, thereby undermining the ability of populations to persist. Pastoral (over-)use of rangeland habitat without sufficient rest periods would clearly represent such a threat (see comments on grazing below). On the other hand, complete lack of disturbance, especially in those sites which are not subject to fire either, such as for example in some small patches of remnant vegetation adjacent to human developments, would result in lack of recruitment, population senescence and decline.

Dependence of recruitment on disturbance points towards poor competitive ability of young seedlings. Degraded landscapes, small patches of remnant vegetation and the boundaries of large reserves onto land under human use usually suffer from edge effects, which include weed invasion; in South Australia, many of these weeds are fast-growing annual broadleaves and grasses tending to quickly dominate their immediate surroundings by densely covering soil surfaces and suppressing other growth. While the effect of weed growth such as annual grasses on *L. saxatilis* was not investigated in this study, the dependence of germination on light and nitrate and the slow growth of seedlings strongly points towards a negative effect of fast growing exotics on its recruitment success. This situation is further complicated by the fact that these weeds often benefit from disturbance as well, making them direct competitors of *L. saxatilis*.

Irrespective of their trigger, for successful growth and maturation, benign conditions for recently germinated seedlings are necessary. Next to a moderation of disturbance, in particular a temporary absence of fire, this calls especially for sufficient soil moisture during summer. However, current predictions of climate change include more frequent fires, higher temperatures and less rainfall. All these factors may adversely affect population persistence of *L. saxatilis*.

**Fig 5-4 Unburnt control site at Telowie**

## *5.5 Monitoring and management in absence of fire*

Where possible, populations should be monitored to record major changes in range, plant numbers, and age structure. Knowledge of the fire histories of populations assists in locating major recruitment events in time (Fig 5-2). In the absence of fire, recruitment activity of the species varies from population to population (Fig 5-4). Where occasional disturbance occurs, gap recruitment will probably be observed. Assessing the age structures of populations aids in deciding whether or not there is a requirement for recruitment management.

Fire is the method of choice where recruitment is insufficient in a senescent population (see Fire Management), but the potential loss of the remaining adults as well as other possible negative impacts on the site have to be taken into account. Where burning is not desired as an initial step, recruitment can be attempted in other ways. As the germination experiment showed, the effect of fire is not primarily linked to heat. Smoke water, light and nitrate are efficient triggers especially if combined, and these effects can be tested in the field as replacement of fire: where seed can be expected to be in soil near adult females, removal of competing vegetation and dense litter, soil disturbance, application of smoke water and nitrate solution, as well as management of herbivory may be worthwhile steps in an attempt to encourage seedling emergence without fire.

Grazing was not included in the project so the following conclusions are tentative, and require further investigation (see “Further Research”). Grazing, being a disturbance that may improve access of light to seed and add nutrients to the soil surface can be viewed as a trigger of germination, so based on the current knowledge, and if applied appropriately, may be well tolerated by the species. Also, adult *L. saxatilis* seem to have enormous growth potential in response to canopy damage and can produce a large amount of biomass in a short time. Assuming palatability and non-toxicity, this germination and growth response could make the species an attractive and viable component of rangeland grazing. However, to maintain this ability, adults need rest periods for regrowth, so periodic grazing followed by recovery periods of low disturbance would probably form the basis of grazing management (Pavlovic 1994). Otherwise, the ongoing broad scale disturbance associated with livestock grazing can easily be seen to lead to population decline: where *L. saxatilis* is originally present in rangeland and then subjected to constant or frequent grazing, ongoing biomass reduction is likely to damage adults, reduce seed set and inhibit seedling establishment. The ongoing disruption of the soil surface exposes seed to the above mentioned non-fire related germination cues of light and nutrient accumulation, leading to germination and initial seedling growth, which is then again removed by grazing and trampling. Such repeatedly unsuccessful recruitment attempts gradually exhaust the soil seedbank. This process is much aggravated by drought, when grazing pressure on remaining vegetation is high, the soil surface lacks vegetation cover and is subject to animal traffic, as multiple disturbances then interact and have destructive results on plant populations (Hobbs and Huenneke 1992). Where adults are in decline but seedling recruitment is still evident, longer periods of rest, possibly aided by exclusion fencing, are likely to greatly assist successful seedling recruitment. If fire and grazing are combined, populations may entirely depend on seedling recruitment, and rest during the primary juvenile period of *L. saxatilis* is paramount, as shown for other woody species (Midgley *et al.* 2010).

# 6 *Further research*

Much of the interpretation of the results calls for the existence of a persistent soil seedbank, and this matter requires some direct investigation. Longevity of seed in the presence of repeated disturbance with or without fire is of particular interest, due to its relevance to the ability of populations to recover from complete loss of plants, possibly even repeatedly before regrowth reaches maturity. An investigation of this matter could involve sampling of seed banks near recently burnt *L. saxatilis* before seed production has recommenced. Soil samples should be collected at various depths to allow for the possibility that some seed may be buried too deeply to be affected by fire.

From these samples, isolation of seed from soil matter could be attempted, although certainly no easy task in view of the small size and inconspicuous appearance of seed, and be followed by viability assessment or germination testing. Alternatively, germination tests involving the entire soil samples may be a quicker and more efficient approach. Such germination tests could be similar to the current study. Some of these samples could be tested repeatedly to capture a potential staggered dormancy release of soil-buried seed. Resistance of some of the seedbank to fire-induced germination would indicate the possibility of greater tolerance to repeated fires in short succession, than it seems likely from results obtained so far.

**Fig 6-1 Germinating seeds of the rare *L. saxatilis* were placed in potting mix once no longer required for the test and many of them grew successfully to planting size**

The variation in resprouting response invites investigations into matters that were outside the scope of the current study and relate to differences in ecotypes (see below), or more likely, external conditions that influenced the ability of the plants to resprout. Investigation of these various factors calls for ongoing *L.saxatilis* fire response monitoring to be accompanied by parallel measurements of matters such as fuel levels, slope, vegetation characteristics, soil moisture and seasonal weather patterns. All these matters potentially have combined effects on fire intensity and/or severity and consequently, the ability of a plant to resprout or not (Borchert and Odion 1995; Odion and Davis 2000; Vivian *et al.* 2008). Carbon storage was identified as a potential contributor to the strong resprouting ability of surviving adults, calling for further investigation. Additionally, seasonal or habitat factors may interact with the amount of such potential carbon within the plant – for example it may be different during the processes of flowering and seed production to the somewhat normally less metabolically active time of late summer. The potential variability in carbon content through the seasons could be investigated through repeated sampling of starch content.

The observed seedling response involved some inconsistency, as seedling recruitment in the absence of fire was much stronger at Telowie than at Mount Remarkable. As detected by the field study, the height and size distributions of *L. saxatilis* also varied between the parks. Clearly this size difference could also be a result of the divergent growth conditions, but the possibility of different ecotypes could be easily investigated by parallel nursery propagation of both populations (Fig 6-1). This would allow a comparison of both their growth characteristics, as previously executed by Benwell and McCorkell 2011, and their germination requirements as in the current study. For the purpose of a direct comparison, seed from both locations should be collected, stored and processed in an identical manner to prevent any confounding influences on seed performance. Should ecotypical differences not be detected, then the reason behind the variability in growth and can be sought in habitat factors. These include a very wide range of factors such as soil, vegetation, and the presence of other triggers such as the previously mentioned smoke from nearby fires, but also the presence of exotic mammals such as goats and rabbits at Telowie. These animals may cause disturbance of vegetation cover and soil through travel, grazing and digging; possibly these processes promoted increased germination and recruitment in this park – such a hypothesis offers another avenue of further investigation.

Research into grazing value and management in pastoral land may be of interest to maintain, or even expand, the range of this species, and would offer both ecological and economic benefits. Such an investigation should involve controlled experiments that are directed at nutritional value, palatability to grazing animals and the ability to recover from canopy damage of varying severity and frequency. Additionally, existing remnant populations in pastoral rangeland could be located and the currently applied grazing strategies recorded, analysed and experimentally varied to optimise productivity.

**Fig 6-2 Habitat of *L. saxatilis* in the Southern Flinders Ranges**

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