Reproductive biology of important invasive plants in the Eastern Cape Province of South Africa

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By

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Abstract

Baker's rule predicts species capable of uniparental reproduction are more likely to establish after long distance dispersal (or introduction in the case of invasive plants), thus the ability to undergo autonomous self-pollination should promote colonization. An investigation into the reproductive biology of eleven invasive species in the Eastern Cape Province of South Africa between 2012 and 2014 showed strong support for Baker's law. Breeding system results showed evidence of self-compatibility in eight species, ten species were capable of autonomous self-pollination, and only three species showed evidence of varying levels of self-incompatibility. These results provide evdence that autonomous self-pollination occurs more frequently among invasive species, self-compatible species more frequently become invasive compared with self-incompatible species and that autogamous species should have a larger invasive range. Co-opting suitable local pollinators may be problematic for invasive plants, especially those with highly specialized pollination systems. The species investigated appear to be largely independent of pollinators, mostly setting seed in the absence of pollinators. Despite this, all eleven invasive plant species are regularly visited by a variety of generalist pollinators including *Apis mellifera*, *Xylocopa* bees and *Allodapini* species. Pollinators all carried substantial pollen loads, even managing to extract pollen from more specialized plants, such as the poricidal anthers of *Solanum* species, and frequently came into contact with both anthers and stigmas. Considering most of theses species are capable of autonomous self-pollination, their reliance on pollinators may be low. Even the most self-incompatible species, *Passiflora caerulea*, appears to have successfully co-opted local pollinators (honeybees and carpenter bees), ensuring successful pollination and seed set. The ability for cross-pollination by local pollinators allows for some degree of genetic variation within invasive plant populations, especially for self-incompatible species. Inadequate pollen deposition by unreliable or inefficient pollinators, or reduced resource availability, can result in pollen limitation. Invasive plant species may be especially susceptible, with three of the plant species investiagted showing possible pollen limitation at the level of seed set, while the remaining nine invasive plant species showed no evidence of pollen limitation in South Africa. The ability to utilize

uniparental reproduction (as Baker's law predicted), and co-opt local pollinators has allowed invasive plants in the Eastern Cape to successfully establish and persist after introduction. Hence, the inclusion of reproductive traits of plants should therefore be included in risk assessments for future plant invaders.

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Declaration

This dissertation, submitted for the degree of Master of Science in the Department of Botany, Rhodes University, represents original work by the author and has not been submitted in any form to any other institution. Where mention has been made of the work of others, it has been duly acknowledged in the text.

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I certify that the above statement is correct.

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Chapter 1: Introduction

1.1 Introduction to invasion biology

The invasion of ecosystems by exotic species has become a major concern globally. Biological invasions not only effect local biodiversity by suppressing or eliminating native species, but may affect ecosystem structure and functioning by for example modifying pollination webs, changing plant-animal interactions and altering plant-seed dispersal mechanisms amongst many others (Bjerknes *et al*, 2007; Kearns *et al*, 1998; Mack *et al*, 2000; Pyšek *et al*, 2004; Rejmánek *et al*, 2005; Richardson, *et al*, 2000a; Traveset and Richardson, 2006). As such the field of invasion ecology has arisen, with the aim of trying to understand invasions, what causes them, how to prevent them and what management practices are best at controlling them.

Alien plant species (‘non-native’, ‘exotic’ species) are characterized as having moved from their native range, due to intentional or unintentional human involvement, to an introduced range where they encounter a new environment, and may rapidly reproduce (Traveset and Richardson, 2006). They need to compete with native species for light, nutrients, space and water and can become aggressive competitors (Levine *et al*, 2003 in Bartomeus *et al*, 2008). Invasive plants encountering a new environment need to overcome: (1) geographical barriers, i.e. individuals need to arrive in the new environment; (2) habitat barriers e.g. different climate regimes; (3) biotic barriers e.g. competition with local flora in order to survive (cf. Le Maitre *et al*, 2004) and (4) reproductive barriers e.g. lack of suitable mates. When plants are able to overcome these barriers they may rapidly reproduce to establish functional populations and successfully persist in an environment (Prentis *et al*, 2008 and references therein). Most introduced species however fail to colonize a new area and fewer successfully overcome the barriers to establishment and spread to the extent that they become invasive (Bjerknes *et al*, 2007; Pyšek *et al*, 2004, 2011; Richardson, and Rejmánek, 2011; Richardson *et al*, 2000a), with the successful ones often being generalists capable of withstanding a broad range of conditions (Bromilow, 2010).

There is much debate around whether we can accurately predict which species may become invasive and what characteristics - such as life history traits - contribute to a species invasive potential (see van Kleunen *et al*, 2010 and Pyšek and Richardson, 2007, for more information). Invasion biologists are still trying to identify potentially invasive species, by creating an 'invasive species syndrome' where species are screened for potential risk using the characteristics of known invaders (Lloret *et al*, 2005). Studies have focused mainly on simple, easily investigated functional traits (van Kleunen *et al*, 2010) such as native range size (Pyšek *et al*, 2009); seed size (Grotkopp *et al*, 2002); growth rate (Kolar and Lodge 2001); and plant fitness (van Kleunen and Johnson, 2007a). There are however limitations, for example, generalizations about the breeding system of invasive plants (i.e. clonal growth, apomixis or autogamy), do not always hold true for all invasive plant species (Baker, 1965; Liu *et al*, 2006). Therefore, the development of an 'invasive species syndrome' is thought to be somewhat unattainable (Rejmanek and Richardson, 1996). Further studies on species attributes, which promote invasive potential, could still however be useful for identifying trends and predicting the potential threat of a plant species.

The success of an invasive plant into its new range depends on its ability to successfully reproduce. If the species is (a) capable of reproducing without pollinators, (b) co-opts local pollinators, and/or (c) adequate pollen is transferred to ensure seed set and prevent pollen limitation, then successful invasion is possible (Harmon-Threatt *et al*, 2009). Entomophilous plants that are self-incompatible will rely entirely on the availability of pollinators for sexual reproduction, compared with species that are self-compatible and can still produce seeds with limited or no mate availability. This is important when colonizing a new area, as pollinators and potential mates are then not required to establish and spread (Correia *et al*, 2014). Self-compatibility also ensures invasive populations continue to expand along their range edge, and when local extinction occurs, they are able to recover (Pannell and Barrett, 1998; Rambuda and Johnson, 2004).

So what makes plant species which are new to an area and have not had the time to evolve so adept at out-competing and displacing native species, which are likely highly adapted to the local conditions at a site? The characteristic's of an invasive species, and a new environment that is susceptible to invasion is thought to assist a plant species establishment (Sax and Brown, 2000). Species with an r-selected strategy, that have a broad range of ecological requirements (e.g. generalist) and an association with disturbed habitats are thought to be good invaders, while environments easy to be easily invaded are those that have been isolated either historically or geographically, have high levels of disturbance, low abundance of native species, and few co-adapted enemies (Sax and Brown, 2000).

Box 1. Definition of Terms

Definition of terms used follow those of Richards (1997) and provide a guide to the terminology used in this study.

Apomixis	Any asexual reproduction in plants; includes vegetative reproduction and agamospermy
Agamospermy	The asexual production of fertile seeds and functional fruit from flowers without fertilization occurring
Autonomous self-pollination	Self-pollination and production of seeds without the aid of a pollen vector
Xenogamy/ Cross-pollination	Pollen from the flower of an unrelated individual is used to fertilize the ovary of another individual
Geitonogamy/ Self-pollination	Fertilization after a stigma is pollinated with pollen from another flower on the same plant, usually through the action of a pollinator or wind
Cleistogamy	Self-fertilization within a permanently closed flower
Self-compatible	Capable of self-pollination
Self-incompatible	Incapable of self-pollination but can utilize pollen from another individual

1.2 Baker's law and the breeding system of invasive plants

Baker's Law suggests that an individual capable of uniparental reproduction is more likely to produce offspring than two self-incompatible individuals after long-distance dispersal (Baker, 1955, 1967). If a single plant or a few individuals which are capable of self-pollination become established after the initial colonization event (from a native population where outcrossing predominates), dominance of self-compatible species would be expected in the new population (Pannell, 2015; Pannell *et al*, 2015). A hermaphroditic species can reproduce from a single introduced individual and is more likely to become established compared to a dioecious species, which would require the introduction of two or more individuals (Baker, 1955, 1967; Rambuda and Johnson, 2004). A self-compatible individual would not suffer mate limitation, allowing for successful establishment and colonization, with or without a co-opted pollinator, a species capable of autonomous self-pollination would ensure sucesssful reproduction without a mate or a pollinator thereby promoting an invasion, while a self-incompatible species would need to find a suitable mate, be in close proximity and rely on either wind and/or finding a suitable pollinator to ensure reproduction and therefore successful colonization (Baker, 1955, 1967; Rambuda and Johnson, 2004; Stebbins 1957). These different compatibility rates allow for invasions by plants to occur under different circumstances. Self-compatible hermaphrodites are therefore thought to be more likely to become invasive compared with dioecious, self-incompatible or obligatory outcrossing species (Baker, 1967; Rambuda and Johnson, 2004; Hao *et al*, 2011).

A population founded in a new environment is isolated, lacking the genetic variability available in the parent population, so outcrossing between all individuals (either by wind or insect pollinators) in the new population would increase gene flow and reduce the risk of negative effects such as inbreeding depression (Carlquist, 1966a,b, 1974). Initially, when the population is small, the ability for self-pollination would give an invader the advantage, but once the population is established and/or pollinators have been co-opted, a mixture of selfing and/or outcrossing could be utilized (Igic *et al*, 2008; Pannell and Barrett, 1998; Rejmánek *et al*, 2005). Outcrossing would therefore be an advantage to invading species, possibly outweighing the initial disadvantages faced during establishment (Pannell and Barrett, 1998). It is not always clear how alien plants (especially the self-incompatible ones) are able to reproduce successfully in new environments, and become invasive (Hao *et al*, 2011; Rambuda and Johnson, 2004).

Self-incompatibility therefore does not necessarily prevent an exotic plant from invading. Self-incompatible plant species may be introduced repeatedly in large numbers e.g. through agriculture, forestry and as ornamentals, and form functional out-crossing populations (Bromilow, 2010). The degree to which invasive plant species are either self-compatible or self-incompatible seems to vary, with studies showing species seen as typical outcrossers can also have low levels of selfing genes which can be ‘switched on’ when necessary, for example during colonization (Brennan *et al*, 2005) though more studies are required to fully understand this concept. Rambuda and Johnson (2004) investigated the breeding system of 17 invasive species in KwaZulu-Natal, South Africa, and found 15 to be self-compatible while 2 where agamospermous. Self-compatibility was also found by Stout (2007b), in the invasive shrub *Rhododendron ponticum* (L.), and Rodger *et al* (2010) found

Lilium formosanum (Wallace) (Liliaceae), to be capable of autonomous self-pollination, but the presence of a pollinator increased seed production. In China, Hao *et al* (2011) found a significantly higher percentage of invasive Asteraceae to be self-compatible and capable of autonomous seed set compared to a global database on Asteraceae and in the Eastern Cape of South Africa, *Araujia sericifera* (Brot.) (Apocynaceae) is an invasive plant with a highly specialized pollination syndrome that has managed to co-opted local honeybees which facilitate either self-pollination or outcrossing, enabling it to set seed (Coombs and Peter, 2010). Species that are able to self-pollinate can undergo multiple extinction and re-colonization events before establishment, which provides reproductive assurance especially in a new, unknown environment (Brennan *et al*, 2005; Pannell and Barrett, 1998). Alternatively, self-incompatibility in the invasive range has been found in some species for example Brennan *et al* (2005) found the weed *Senecio squalidus* (L.) (Asteraceae) to be self-incompatible in the United Kingdom and Hong *et al* (2007) found *Mikania micrantha* (Kunth) (Asteraceae), an invasive weed in China to be reliant on pollinators for seed set. In Florida, USA, the invasive plant species *Paederia foetida* (L.) (Rubiaceae) was found to be self-incompatible, relying on native Halictids and introduced European honeybee for seed set. This ability to outcross minimizes the negative effects associated with deleterious mutations, which could affect the adaptability of offspring (Brennan *et al*, 2005). To combine this, the Brazilian water hyacinth, *Eichhornia paniculata* (Spreng) (water hyacinth), is self-incompatible in its native range (with low levels of a self-compatibility gene) yet in the invasive range there is a significant increase in the frequency of self-compatibility among individuals (Prentis *et al*, 2008; Barrett *et al*, 2008), therefore mating strategies can shift between outcrossing and selfing (Brennan *et al*, 2005), with more research being required to understand the mechanisms involved in the breeding system of invasive plants.

Self-compatibility was found to be less common in a study of 142 invasive species in the USA compared with non-invasive species (Sutherland, 2004; van Kleunen *et al*, 2008); another study of invasive European species in the USA found those capable of autonomous self-pollination had a wider invasive range (van Kleunen and Johnson, 2007b); and a study of Iridaceae showed those capable of autonomous self-pollination were more likely to become invasive compared species not capable of autonomous self-pollination (van Kleunen *et al*, 2008). Support Baker's Law is therefore equivocal (Pyšek *et al*, 2011; van Kleunen *et al*, 2008) making it difficult to predict a plants invasive potential based on breeding system traits alone.

1.3 Importance of pollinators in facilitating invasions

The majority of angiosperms rely on pollinators for reproductive success and ultimately seed production (Waser *et al*, 1996). In return insects are rewarded with resources notably pollen and nectar (Vilà *et al*, 2009). What role however, do pollinators play in ensuring successful reproduction of invasive plant species?

When encountering a new environment it is often crucial for invasive plants (especially self-incompatible species) to find suitable mates, of the same species, with viable pollen, and/or pollinators to facilitate the movement of pollen from anther to stigma (Harmon-Threatt *et al*, 2009; Richardson, *et al*, 2000a). Finding suitable pollinators can be achieved by either (a) bringing mutualist pollinators from the native range (b) co-opting resident pollinators in the new range (c) waiting for a specialist pollinator to be introduced, for example with *Ficus microcarpa* L.f. (Bjerknes *et al*, 2007; Harmon-Threatt *et al*, 2009; Parker and Haubensak, 2002; Richardson *et al*, 2000a) or (d) waiting until selection produces traits in the plant that are suitable to the available pollinators.

A common idea in pollination biology was that animal-plant interactions were mainly specialized but evidence now suggests most plants fall on a continuum between specialization and generalization (Johnson and Steiner, 2000; Waser *et al*, 1996). Stebbins 'most effective pollinator principle' states plants are most likely to specialize with the most effective and/or abundant pollinator, at times when pollinators are most consistent (Johnson and Steiner, 2000; Stebbins, 1970), whereas generalization in plant pollinator systems is predicted when variation in pollinators is a function of the system (Waser *et al*, 1996; Johnson and Steiner, 2000). Generalization is seen as being common among short-lived plants which rely on pollinators for seed set, while the more specialized species are the converse, being long-lived or reproducing vegetatively (Johnson and Steiner, 2000). Further, abundance, breeding system, plant life history and successional status are seen as driving specialization in plants (Johnson and Steiner, 2000). Generalized plants are therefore seen as being capable of attracting; rewarding and using a wide range of pollinators while highly specialized plants rely entirely on a single pollinator or a small suite of pollinators (Waser *et al*, 1996).

According to 'Bakers rule' plants with a generalized pollination system, or one requiring no pollinators, is more likely to become invasive than those which are specialized, as they can easily co-opt local pollinators from the broad range that is available, to guarantee reproductive success (Baker, 1965, 1974; Johnson and Steiner, 2000; Rambuda and Johnson, 2004). Highly specialized plants are thought to be less likely to encounter a particular pollinator in the invasive range, unable to set seed, and therefore less likely to become invasive (Rodger *et al*, 2010). 'Baker's Law' further predicts invasive species need not rely heavily on pollinators as their breeding systems usually enables reproduction in the absence of a mate and/or pollinators but evidence is mounting that suggests even self-compatible invasive species still rely on pollinators for reproduction (Liu *et al*, 2006; Hong *et al*, 2007; van Kleunen and Johnson, 2005 and see references in Ward and Johnson, 2013).

Few invasive species however appear to be limited in spread by the absence of pollinators, as even plants with highly specialized pollination syndromes can co-opt local generalist pollinators (Richardson *et al*, 2000b). A highly specialized plant may encounter pollinators from the same family or functional group in the new range or co-opt an introduced species that is effective, enabling successfully reproduction (Liu and Pemberton, 2009). Another way to overcome specialization is to switch pollinators (Valentine, 1977 in Rodgers *et al*, 2010) or have uniparental reproduction therefore pollinator specialization does not guarantee that a plant will not become invasive (Rodgers *et al*, 2010).

Invasive species that have become successful come from a variety of backgrounds, and have managed to become successful invaders, co-opting both native and non-native pollinators that ensure reproduction. *Gomphocarpus physocarpus* (E. May.) (milkweed) is self-incompatible in South Africa (the native range), relying on a variety of wasps from the genera *Belongaster* and *Polistes* for pollination. Mechanical reconfiguration of the pollinaria is required before being deposited, limiting self-pollination (Coombs *et al*, 2009). Milkweeds are said to have a specialized pollination system yet in Australia three species (*Asclepias curassavica* (L.), *Gomphocarpus fruticosus* ((L.) W. T. Aiton.) and *G. physocarpus*) have become invasive. These species are self-compatible and rely on various species of Hymenoptera (*Gomphocarpus* species) and Lepidoptera (*A. curassavica*) for pollination and successful seed set, contradicting the idea that a specialized pollination system inhibits invasion (Ward and Johnson, 2013). Native to Spain, *R. ponticum* is naturalized in Ireland and Britain, where introgression with North American *Rhododendron catawbiense* (Michx.), *Rhododendron maximum* (L.) and an unknown species has occurred (Stout, 2007 a,b). Flowers are self-compatible and have low levels of autonomous self-pollination but exposure to pollinators increased seed set, with native generalist species being attracted to the rich nectar and pollen reward though bumblebees are the only species effectively depositing pollen on stigmas (Stout, 2007a,b), and the buzz pollinated invasive *Solanum torvum* (Sw.), (Turkey Berry) in Florida, USA, was pollinated more effectively by the introduced orchid bee *Euglossa viridissima* (Bembé and Eltz.), than native species of Halictidae. Studies have therefore shown that introduced plants can successfully co-opt resident pollinators (native or alien) and are efficiently pollinated by them (Harmon-Threatt *et al*, 2009; Morales and Aizen 2006; Richardson *et al*, 2000b; Vilà *et al*, 2009).

Many invasive species produce abundant floral rewards to attract pollinators by producing abundant flowers, secreting large volumes of nectar or by having longer flowering periods such that resources are available for an extended period of time (Ward and Johnson, 2013). Alien plants have both positive and negative effects on native plant and pollinator populations, with invasive species often outcompeting native plants resulting in negative impacts on native populations - namely decrease in seed set, seed quality, population size growth and/or genetic structure (Traveset and Richardson, 2006). When alien plants affect pollination of native plants in a positive way, it can either be through effects on pollinator populations or by altering pollinator behavior (Bjerknes *et al*, 2007). Alien plants can increase the population size of pollinators by increasing the availability of resources, thereby sustaining or increasing native plant populations for longer periods, for example different flowering times of native and alien plants means pollinator populations persist, facilitating the pollination of native plant species earlier or later in the flowering season. In contrast, alien plants can cause a decrease in native plant populations, with some native pollinators relying almost exclusively on the invasive plants for resources (Bjerknes *et al*, 2007).

The effect on pollinator behaviour of invasive plants can occur in three ways. Firstly facilitation, whereby alien plants increase the resources available to pollinators, making populations more attractive – otherwise known as the “magnet species effect” (Bjerknes *et al*, 2007; Laverty, 1992). This can result in increased number of visits by pollinators to native species resulting in increased pollen deposition and seed set. Secondly, invasive plants could negatively compete with native species, by being preferred by pollinators (Bjerknes *et al*, 2007). This would result in a decrease in visits to native species, an increase in heterospecific pollen deposition and a decrease in conspecific pollen deposition, leading to a decrease in seed set of native species (Bjerknes *et al*, 2007). Thirdly, there may be no difference in pollinator behaviour between alien and native species, as visitation rates might not change much, or if pollinator switch does occur from native to invasive species, other generalist pollinators might fill the role, compensating for the loss of a pollinator (Bjerknes *et al*, 2007) though this could alter the quality of visits not the quantity. It is therefore important not to look only at the pollinators but also their behaviour, abundance and effectiveness when trying to understand pollination systems (Ward and Johnson, 2013).

To date, our understanding of how pollination mode and availability of pollinators affects plant invasions is poorly understood (Pyšek *et al*, 2011). Overall, co-opting local pollinators in a new environment is not the only problem invasive plants face, as new pollinators might not be as effective as local pollinators in transferring pollen effectively to the stigma. This will result in problems with the quality and quantity of pollen received, which could result in pollen limitation (Parker, 1997; Harmon-Threatt *et al*, 2009; Richardson, 2004, Aizen and Harder, 2007)

1.4 Into the unknown: are invasive plants pollen limited or not?

Pollen limitation affects a plants reproductive success, resulting in fewer fruits and/or seeds being produced, due to inadequate pollen deposition or too few resources, to ensure maturation of fruit/seeds (Abdala-Roberts *et al*, 2014; Burd, 1994; Knight *et al*, 2005; Larson and Barrett, 2000). Pollen limitation can be due to 'quantity limitation' whereby stigmas receive too few pollen grains to enable adequate fertilization, or 'quality limitation' whereby pollen grains received are of a poor quality e.g. self-pollen (Ashman *et al*, 2004; Parker and Haubensak, 2002). Furthermore, the theory of sexual selection predicts female reproductive success is limited by availability of resources rather than pollen receipt (Knight *et al*, 2005) and that seeds produced should mature without limitation (Haig and Westoby, 1988; Knight *et al*, 2005, 2006), however this is not always the case. Pollinators play an important role in the reproductive success of plants, with one directly affecting the other (Parker and Haubensak, 2002).

One way for plants to escape from pollen limitation is to reproduce without dependence of pollinators, for example through self-compatibility (Morgan and Wilson, 2005). Being capable of autonomous self-pollination releases the plant from the need for a mate or pollen vector i.e. during the invasion process when mates and/or pollinator availability may be low (Larson and Barrett, 2000; Parker and Haubensak, 2002). This mode of reproduction is said to have evolved in areas were pollinator visitation was infrequent or inadequate (Larson and Barrett, 2000) and would apply to invasive species when they encounter a new environment where they have not co-evolved with the local pollinators, meaning the potential pollinators might not be available or are inadequate, possibly leading to pollen limitation (Richardson *et al*, 2000b). Changes in pollinators resulting from differences in pollinator assemblages, population dynamics of pollinators or differences in plant species composition in an area can all affect the reproductive success of a plant, and therefore the degree of pollen limitation a plant might experience (Parker and Haubensak, 2002). Founder populations of invasive plant species are likely to be small, and possibly fragmented, meaning they will suffer from the founder effect due to fewer mates and/or suitable pollinators. This can result in pollen limitation, as pollinator visitation and pollen deposition rates will decrease (Davis *et* al, 2004; Knight *et al*, 2005; Ward and Johnson, 2005; Zhang and Lou, 2015).

Pollen limitation however occurs in a diverse range of species, with different life histories and breeding systems (Ramsey, 1995), and studies have shown species to be pollen limited at the population level, between sites and even within years (Ashman *et al*, 2004; Burd, 1994; Fulkerson *et al*, 2012; Knight *et al*, 2005, 2006). Plant species may also suffer pollen limitation due to resource limitations such pollen availability, light, variable climate, water, size and density of plant populations, habitat fragmentation and the previous years resource allocations (Fulkerson *et al*, 2012; Ward and Johnson, 2005).

Pollen limitation is thought to have little effect on invasive plants (Richardson *et al*, 2000). Few studies exist that specifically focus on the pollen limitation of invasive plant species and as such, there is limited data to detect possible patterns of the effect of pollen limitation on invasive plant species (Harmon-Threatt *et al*, 2009). Pollen limitation in invasive plants could therefore have important effects, either constraining or facilitating invasions (Harmon-Threatt *et al*, 2009; Knight *et al*, 2005; Parker and Haubemsak, 2002). One example is from Ireland, where the exotic *Rhododendron ponticum* was found to not be pollen limited, as no difference was observed between pollen supplemention and control treatments (Stout, 2007).

1.5 Invasive plant problem from a South African perspective

South Africa has one of the most unique floras in the world, with three biodiversity hotspots situated in our country. One of these is the Maputaland-Pondoland-Albany hotspot that includes the Eastern Cape Province. As with the rest of South Africa, the Eastern Cape is not exempt from plant invasions. In South Africa over R6.5 billion is spent trying to control invasive plant species (Wilson *et al*, 2013) and over R10 billion is lost annually due to invasion of agricultural land, and the expense of trying to control invaders (Le Maitre *et al*, 2004). Of the approximately 8750 introduced plant taxa, only 198 are listed in legislation and 62 are regularly controlled with Working for Water (WfW) being developed by the Department of Agriculture and Forestry as a means of controlling invasive plant species by physical and chemical removal, especially from waterways (Wilson *et al*, 2013).

Finding characteristics or a 'plant syndrome' that aids plant invasion could therefore help identify key features for risk assessments concerning future plant invasions (Pyšek and Richardson, 2007; Rejmánek *et al*, 2005). Studies in South Africa focusing on reproductive biology of invasive plant species by Rambuda and Johnson (2004) who looked at 11 invasive species in KwaZulu-Natal and Moodley *et al* (2015) on *Banksia* and *Hakea* in the Western Cape, both found invasive species capable of autonomous self-pollination, and that these generalists co-opt local honeybees as pollinators. In South Africa, Rodger and Johnson (2013) found *Acacia dealbata* (Link), to be capable of autonomous self-pollination, being partially self-compatible. Dispersal of the highly invasive *Melia azedarach* (L.) seeds in South Africa by seven native bird species and one bat species, may help disperse invasive seeds to favourable sites, though germination in the field was lower versus germination in the greenhouse (Voigt *et al*, 2011). These studies show invasive plant species in South Africa show a trend towards being self-compatible, capable of autonomous self-pollination, generalists that easily co-opt local honeybees and produce fruit which is easily dispersed by native frugivores. As detailed above, the ability to self-pollinate and a generalized pollination system are common features among invasive plant species worldwide.

1.6 Aims and objectives

The overall aim of this project was to investigate the reproductive traits and pollinator dependence of 11 invasive plants in the Eastern Cape Province of South Africa to test the following hypotheses:

I. Baker's Law predicts species capable of uniparental reproduction are more likely to successfully invade a new environment compared to those that are self-incompatible and rely on pollinators for outcrossing. I tested the hypothesis that all study species would be self-compatible and capable of uniparental reproduction.

II. Generalist invasive plant species are more likely to successfully co-opt local pollinators to ensure successful reproduction, negating the need for pollinators for seed set. I tested the hypothesis that the study species have successfully co-opted native pollinators and that pollinators are important for seed set.

III. Invasive species with the ability to reproduce via self-pollination are less likely to exhibit pollen limitation from inadequate visits by co-opted local or foreign pollinators. I tested the hypothesis that the study species are not pollen limited due to adequate pollen deposition by native pollinators or due to autonomous self-pollination.

Chapter 2: Study species

2.1 Background to Study species

Each biome in South Africa has different plant invaders due to the varying environmental conditions (Henderson, 2007). A number of invasive plants that are problematic in southern Africa also occur in the Eastern Cape. The species chosen for this study have all had relatively long establishment times, though *Yucca aloifolia* (L.) has only recently been reported as naturalized in South Africa (Smith *et al*, 2012). Little is known about the reproductive biology of these species in their invasive range, especially in the Eastern Cape province. Their locality in and around Grahamstown, and their population size, made these species suitable candidate species for study. *Acacia longifolia* ((Andrews)Willd.) and *Melia azedarach* (L.) can be found along verges, while the *Opuntia* species invade farmland and natural vegetation around Grahamstown (Figure 2-1, F). *Solanum chrysotrichum* (Schltdl.) is mainly found around the Kei Mouth area of the Eastern Cape, forming dense stands with *Solanum mauritianum* (Scopoli), while *Passiflora caerulea* (L.) and *Pereskia aculeata* (Mill.) commonly occur along roadsides and on fences in and around Grahamstown.

Table 2-1: Background information on 11 study species selected in the Eastern Cape for the current study. Growth form, native range, local distribution and NEMBA** classification is given for each species. SA: South Africa. References: Henderson (2001)[a] Welman (2003)[b] Paterson *et al*, (2011)[c] Smith *et al*. (2012)[d]. Provinces of South Africa include: WC: Western Cape, EC: Eastern Cape, KZN: KwaZulu-Natal, FS: Free State, NW: North West, MP: Mpumalanga, GP: Gauteng, LP: Limpopo.

Plant Species	Family	Growth Form	Native range	SA Distribution	NEMBA**
Acacia longifolia (Andrews) Willd.	Fabaceae	Shrub or tree	Australia/ Tasmania[a]	WC, EC, KZN, MP	1b
Melia azedarach L.	Meliaceae	Tree	India to Australia[a]	Throughout SA except arid west	1b
Opuntia aurantiaca Lindl.	Cactaceae	Succulent shrub	South America[a]	EC, FS, KZN, LP	1b
Opuntia ficus-indica (L.) Mill.	Cactaceae	Succulent shrub or tree	Tropical America[a]	Throughout SA	1b
Opuntia monacantha Haw.	Cactaceae	Succulent shrub or tree	South America[a]	Coastal EC, WC, KZN	1b

Plant Species	Family	Growth Form	Native range	SA Distribution	NEMBA[**]
Opuntia stricta (Haw.) Haw	Cactaceae	Succulent shrub	Central and North America [a]	WC, EC, FS, KZN, NW, LP, MP, GP	1b
Passiflora caerulea L.	Passifloraceae	Perennial climber	South America [a]	Coastal WC & EC, GP	1b
Pereskia aculeata Mill.	Cactaceae	Shrubby to clambering vine	South and Central America, West Indies [b]	Coastal EC & KZN, NW, LP, GP	1b
Solanum chrysotrichum Schltdl.	Solanaceae	Shrub or tree	Central America [c]	Coastal EC	1b
Solanum mauritianum Scopoli	Solanaceae	Shrub or tree	South America [a]	WC, EC, KZN, GP, LP, MP	1b
Yucca aloifolia	Agavaceae	Shrub or tree	Central and southern North America [d]	Eastern Half	Not listed

[**] According to the National Environmental Management: Biodiversity Act 10 of 2004; Category 1b: Invasive species requiring control and removal by means of an invasive species management programme.

2.1.1 *Acacia longifolia* (Andrews) Willd.

Biology

Acacia longifolia (long-leafed wattle, Fabaceae) is an evergreen tree or shrub 8 to 20 m that is native to south-eastern Australia and Tasmania (Table 2-1) (Henderson, 2001; Marchante *et al*, 2010). Leaves are absent in adults and replaced by phyllodes which are light green, max 180 mm in length with prominent longitudinal veins. Inflorescence consists of cylindrical heads (50 mm long, 7 mm wide) with yellow flowers (Figure 2-1, A), which protrude from the leaf axil (Kodela and Harden, 2002). Pale brown pods 4 - 15 cm long are straight to twisted, constricting between seeds. Pods are leathery when immature, becoming papery and brittle when dry (Henderson, 2001; Kodela, and Harden, 2002). Seeds are small (2 - 2.5 mm), elliptical, shiny, with 4 - 6 seeds per pod (Marchante *et al*, 2010). The seeds have an elaiosome for attracting ants, which bury the seeds (Marchante *et al*, 2010; Willson and Traveset, 2000). In South Africa, it is easily identified by brownish-coloured galls (Figure 2-1, B), occurring in place of flower and leaf buds, which are produced by the biological control agent *Trichilogaster acaciaelongifoliae* (Froggatt), a Hymenoptera species (Dennill *et al*, 1993; Henderson, 2001; Marchante *et al*, 2011).

A. longifolia is self-incompatible in its native range, only setting fruit when pollinators move between individuals (Bernhardt, 1987), though low levels of selfing produced viable seeds in

Portugal where the species is invasive (Correia *et al*, 2014; Gibson *et al*, 2011). In Australia, where *Apis mellifera* (Linnaeus) is introduced, and South Africa and Europe where *Acacia longifolia* is introduced, honeybees pollinate flower heads by scraping the anthers with their forelegs, to remove the polyads (or fused pollen grains) (Bernhardt, 1987), and this behaviour was observed in both the native and invasive range (Gibson *et al*, 2011).

Introduced range

A. longifolia is listed as invasive in Argentina (Stellatelli *et al*, 2013), Australia (where it has become locally invasive, spreading from dune habitat to coastal wetlands around Discovery Bay) (Huebner, 2014) and Portugal (Correia *et al*, 2014; Marchante *et al*, 2010). In South Africa, *A. longifolia* was first planted in the Cape of South Africa by British colonists in 1827 (Dennill and Donnolley, 1991) and was only reported as problematic in 1945 (Bromilow, 2010). See Table 2-1 for current distribution in South Africa.

2.1.2 *Melia azedarach* L.

Biology

Melia azedarach (Syringa or Chinaberry, Meliaceae) has a large native range extending from India, across Asia and into Australia (Table 2-1). This deciduous tree reaches up to 23 m in height (Henderson, 2001). Flowers are small (± 10 mm long) and arranged in large terminal, heavily perfumed sprays. Flowers are a light lilac colour, turning deep purple upon maturity (Figure 2-1, C). Ovaries are superior with five to eight locules, each with two or more ovules. Ten anthers are situated on the inner flower (Hau and Mabberley, 2008; Henderson, 2001). Fruit is in the form of abundant immature green fleshy drupes (average diameter of 13 mm), eventually becoming yellow and wrinkled upon maturity (Corlett, 2005; Henderson, 2001). Drupes contain between one and six seeds (average seed diameter of 9mm) (Corlett, 2005; Mabberley, 1984; Vines, 1960).

M. azedarach is capable of self- and cross-pollination (Mabberley, 1984; Waggy, 2009), and autonomous self-pollination (Rambuda, 2001). The fragrant flowers of *M. azedarach* suggest insect pollination, possibly by moths and bees, although it appears pollinators have not been documented for either the native or invasive range (Rambuda, 2001; Waggy, 2009). Studies have shown that *M. azedarach* is capable of reproducing vegetatively from stumps or roots, even after undergoing physical damage e.g. fire, herbivory or mechanical removal (Menvielle and Scopel, 1999; Tourn *et al*, 1999).

Introduced range

M. azedarach is a highly variable species, becoming increasingly invasive in many tropical and subtropical regions of the world (Mabberley, 1984 and Space *et al*, 2000 in Voigt *et al*, 2011; Henderson 2001). Cultivars were introduced for ornamental purposes and shade in many parts of the world, including North and South America, the Mediterranean basin and Africa (Mabberley, 1984; Voigt *et al*, 2011). The invading form in southern Africa is believed to have originated from northern India (Henderson, 2001; Mabberley, 1984). It was first recorded in Cape Town in 1800 (Smith, 1966; Voigt *et al*, 2011) and later (1894) in present day KwaZulu-Natal (Bromilow, 2010). It is highly invasive in the warm eastern coastal regions and northern interior of South Africa (Table 2-1) (Henderson, 2001), commonly invading streams, railway embankments, waste areas, open urban spaces, roadsides and forest fringes (Bromilow, 2010; Henderson, 2001; Voigt *et al*, 2011).

The invasive range includes many parts of Africa, America (Ding *et al*, 2006), the Central Mediterranean region (Crosti *et al*, 2007a,b), Argentina (Pavé *et al*, 2009; Szewczuk *et al*, 2003; Tourn *et al*, 1999; van Wyk and van Wyk, 2009a), Israel (Korine *et al*, 1998), Indonesia (Syamsuwida*, et al*, 2012), in Japan it is listed as naturalized (Nakamoto *et al*, 2009), has been introduced to Brazil (de Nardo *et al*, 1997), and it is widely cultivated for ornamental purposes in Chile (Chiffelle *et al*, 2009).

2.1.3 *Opuntia aurantiaca* Lindl.

Biology

Opuntia aurantiaca (jointed cactus, Cactaceae) is a low growing 0.3 - 1.5 m succulent shrub consisting of numerous branched cladodes (Henderson, 2001; Nieman, 1991). Green cladodes are cylindrical and slightly flattened (Figure 2-1, D). Long, barbed spines (1 - 3 cm) protrude from the cladodes (Figure 2-1) (Henderson, 2001). Flowers are bright yellow, opening mid spring to early summer, and lasting one day (Henderson, 2001). Fruit is in the form of succulent red berries with seeds (Figure 2-1, D) (Henderson, 2001). Stamens are positively thigmotrophic. Thigmotropism is the unidirectional movement of stamens in response to a stimulus. Stamens usually bend inwards towards the stigma upon stimulation, but outward movement has been documented in some species (Cota-Sández *et al*, 2003; Grant and Hurd, 1979). Inward movement of stamens (as commonly seen in *Opuntia* species) is thought to either facilitate pollen deposition on visiting insects or ensure pollinators come into direct contact with stigmas by making insects exit up and over the stigma (Grant and Hurd, 1979), or to facilitated self-pollination (Pimienta-Barrios and del Castillo, 2002), and pollen and/or nectar is the reward (Daumann, 1930; Grant and Hurd, 1979; Lenzi and Orth, 2011).

Native *O. auranatiaca* are said to be agamospermous (Figure 2-1, D) (Archibald, 1936), possibly reproducing via apomixis (Mondragon-Jacobo, 2001), few, if any, viable seeds are formed (Archibald 1936), and growth is mainly by vegetative means (Archibald, 1936; Burdon and Marshall, 1981). There are no know pollinators but one can assume small hymenopterans are the main pollinators (Reyes-Aguëro *et al*, 2006).

Originally from South America, specifically Eastern Argentina and Southern Uruguay, *O. aurantiaca* is believed to be a hybrid of *Opuntia discolor* (Britton and Rose) and *Opuntia sahniana* (Parmentier), although the latter may itself be a sterile hybrid (Moran *et al*, 1976; Moran and Zimmermann, 1991), leaving the taxonomy unresolved (Moran and Zimmermann, 1991).

Introduced range

O. aurantiaca has successfully invaded both South Africa and Australia (Auld *et al*, 1983; Moran and Zimmermann, 1991). It has a long history in South Africa, arriving in the early 1840s from greenhouse collections in the United Kingdom (Zimmermann *et al*, 2004). It was first introduced to a farm in the Stockenstroom district of the Eastern Cape and was later spread around South Africa by missionaries (Bromliow, 2010). By 1892 it had formed dense thickets that were impenetrable to livestock, and with the long spines on cladodes (as seen in Figure 2-1, D) it easily attached to livestock causing injury (Bromilow, 2010; Moran and Zimmermann, 1991; Zimmermann *et al*, 2004). In 1935 the biological control agent, *Dactylopius austrinus* (De Lotto), was released on *O. aurantiaca*, and by 1946 population numbers had decreased, with population numbers going through a 10 - 12 year cycle of expansion and contraction (Zimmermann *et al*, 2004). Table 2-1 shows the current distribution of *O. aurantiaca* South Africa.

2.1.4 *Opuntia ficus-indica* (L.) Mill.

Biology

Opuntia ficus-indica (prickly pear, Cactaceae), originally from Tropical America was first domesticated in central Mexico, with no forms existing in the wild (Table 2-1). It is thought to be derived from *Opuntia megacantha* (L.) though this is contested (Mondragon-Jacobo and Bordelon, 1996; Reyes-Agüero *et al*, 2005).

This succulent, branched, shrub or tree varies in height (max 3 m), often developing a sturdy trunk with age (Figure 2-1, F). Cladodes are flattened, green grey in colour, varying in appearance - some are heavily spined, others spineless (Figure 2-1, F) (Henderson, 2001; Reyes-Agüero *et al*, 2005). Buds emerge in spring, taking 3 - 5 weeks to bloom (Wessels and Swart, 1990; Reyes-Agüero *et al*, 2006). Flowers vary in colour, from yellow, to orange and red (Mondragon-Jacobo and Bordelon, 1996), occurring on the apical margin of cladodes, usually with 10 flowers per cladode, and only last one day (Figure 2-1, E) (Barbera *et al*, 1991, 1992; Henderson, 2001; Mondragon-Jacobo and Bordelon, 1996; Reyes-Agüero *et al*, 2005). Stamens are positively thigmotrophic (see *O. aurantiaca* for description) (Pimienta-Barrios and del Castillo, 2002). Fruit is a fleshy berry, starting out green (Figure 2-1, E), later turning reddish (± 80 mm long), and are covered in clusters of small glochids (Henderson, 2001; Mondragon-Jacobo and Bordelon, 1996; Reyes-Agüero *et al*, 2005). Fruit contains 50 to over 300 seeds, and seed number positively correlates with fruit size (Barbera *et al*, 1991; Mondragon-Jacobo and Bordelon, 1996). Fruits contain both viable (black) and non-viable (brown) seeds (Mondragon-Jacobo and Bordelon, 1996).

O. ficus-indica reproduces sexually - even exhibiting self-compatibility - and asexually, however vegetative propagation is suggested to be the more efficient means of reproduction (Grant *et al*, 1979; Reyes-Agüero *et al*, 2005). In South Africa, honeybees are thought to visit *O. ficus-indica* flowers and some local bird species (Beinart and Wotshela, 2012), and in Sicily, 314 insects were collected visting *O. ficus-indica*, including Coleptera and Hymenoptera (Lo Verde and La Mantia, 2011), though no bee species has been directly linked to *O. ficus-indica* in its native range (Reyes-Agüero *et al*, 2005).

Introduced range

O. ficus-indica was introduced to South Africa at least 250 years ago, infesting more than 900 000 ha of land before a biological control was released (Zimmermann and Moran, 1991). Currently, it is cultivated as stock fodder, and fruit is consumed locally (Beinart and Wotshela, 2012; Zimmermann and Moran, 1991). The spread of *O. ficus-indica* to the Eastern Cape province was either via animals or settlers, possibly as far back as 1750. Once established, *O. ficus-indica* began spreading rapidly and by 1850, it was widely dispersed in the province (Beinart and Wotshela, 2012). Today, it is considered an emerging invasive in the Drakensberg Alpine Centre (Carbutt, 2012). Table 2-1 shows the current distribution of *O. ficus-indica* in South Africa.

O. ficus-indica is currently cultivated in more than 20 countries for fruit and as stock fodder (de Cortázar and Noble, 1992), but the great invasive potential can quickly outweigh the benefits. It is invasive in Tunisia, Morocco, Algeria, Italy, Portugal, France, Germany, Spain, South Africa, Greece, England, United States, Brazil, Argentina, Botswana, Chile, Mexico, Colombia, Guatemala, Puerto Rico, Venezuela, China, the Cape Verde archipelago, Ethiopia, Madagascar, Eritrea and Israel (Asensi *et al*, 2014; Beccaro *et al*, 2014; Casas and Barbera, 2002; de Cortázar and Noble, 1992; Erre *et al*, 2009; Le Houérou, 1996; Liu *et al*, 2006; Lo Verde and La Mantia, 2011; Marco *et al*, 2010; Medina *et al*, 2007; Mondragon-Jacobo and Bordelon, 1996; Nefzaoui, 2010; Pretto *et al*, 2010; Reyes-Agüero *et al*, 2005; Romeriras *et al*, 2011; Tibe *et al*, 2008; Zimmermann *et al*, 2004). Like many of these countries, *O. ficus-indica* arrived in Australia from Rio de Janeiro in the 17th century, with the idea that a cochineal industry could be started. This idea failed as the cochineal insect struggled while the prickly pear thrived, becoming one of the worst invaders in Australia (Mondragon-Jacobo and Bordelon, 1996). The unusual morphological features, its edible properties, the presence of the cochineal insect (i.e. for red dye) and its ability to survive long sea journeys and still produce roots made it favourable to explorers, aiding its global spread (Barbera, 1995; Barbera *et al*, 1992; Mondragon-Jacobo and Bordelon, 1996; Reyes-Agüero *et al*, 2005).

2.1.5 *Opuntia monacantha* (Willd.) Haw.

= *Opuntia vulgaris* Mill. (synonym, misapplied in some instances) (Leuenberger, 1993)

Biology

Opuntia monacantha (drooping prickly pear, Cactaceae) is native to Brazil, Argentina, Paraguay and Uruguay, where it commonly occurs along the coast (Table 2-1) (Henderson, 2001; Lenzi and Orth, 2012; Taylor and Zappi, 2004). This succulent shrub or tree (1 - 3 m) usually has a thick woody main trunk and is much branched, with drooping upper segments consisting of cladodes (Figure 2-2, F). Cladodes are relatively thin, flattened, bright green and often shiny (± 4 cm) with 1 - 3 spines whereas trunks can have upwards of 10 spines, with numerous glochids (Figure 2-2, F) (de Moraes Calvente and Andreata, 2007; Henderson, 2001; Lenzi and Orth, 2012).

Flowers are shallow, bright yellow, 70 - 100 mm in diameter, with stripped red markings on outer perianth (Figure 2-2, C and D) (Henderson, 2001; Lenzi and Orth, 2012). The lobed stigmas become receptive for 10 hours a day upon anthesis (Figure 2-2, C and D). Stamens are arranged in a whorl and are positively thigmotrophic (see *O. aurantiaca* for description) (de Moraes Calvente and Andreata, 2007; Lenzi, 2008; Lenzi and Orth, 2012). Fruits are fleshy, conical to obovoid, 50 - 75 mm long, 40 - 50 mm wide, reddish-purple in colour with numerous clumps of glochids (Figure 2-2 E) (Henderson, 2001; Lenzi and Orth, 2012). Fruits take 240 to 428 days to fully mature (Lenzi and Orth, 2012; Reyes-Agüero *et al*, 2006). Seeds are small, hard and numerous, with black (fertile) and brown (infertile) seeds (Lenzi and Orth, 2012).

In its native range (Brazil), *O. monacantha* is self-compatible but fruit and seed set is significantly greater with cross-pollination (Lenzi and Orth, 2012), and a variety of species including bees, ants and beetles visited the flowers of *O. monacantha*, with bees coming into direct contact with the stimga and mostly collected pollen as a reward (Lenzi and Orth, 2012). In the French Mediterranean, where *O. monacantha* is naturalized, six bee species reguarly visited flowers including *A. mellifera, Xylocopa* spp and Halictids (Daumann, 1930 in Grant and Hurd, 1979). Rooting and budding of fruit occurs, suggesting asexual reproduction (Lenzi and Orth, 2012).

Introduced range

In South Africa, *O. monacantha* was present in the Western Cape by 1772, and by the early 1890s, it was considered a serious pest having rapidly spread along the east coast (Table 2-1) (Zimmermann *et al*, 2004). In India and Sri Lanka the destructive success of the cochineal insect in controlling *O. monacantha* came to the attention of Australians and South Africans who were trying to manage large infestations (Zimmermann *et al*, 2009). This prompted the use of the biocontrol agent (*Dactylopius indicus* (Green), an Hemiptera) to be released in 1913 with great success (Moran and Zimmermann, 1991; Zimmermann *et al*, 2004).

O. monacantha has spread to central and south eastern USA, throughout Asia, Africa, Madagascar, Australia, New Zealand, India, Sri Lanka and on many islands in the Pacific, Indian and Atlantic oceans (Chaudhry *et al*, 2001; Heenan *et al*, 2002; Labra *et al*, 2003; Liu *et al*, 2006; McNeely, 2001; Zimmermann *et al*, 2004).

2.1.6 *Opuntia stricta* (Haw.) Haw.

Biology

Opuntia stricta (erect prickly pear, Cactaceae) is native to Central and North America, the Caribbean and West Indies (Henderson *et* al, 1987; Henderson, 2001; Rambuda, 2001; Stamer *et al*, 1987). This large, spreading, much branched, spiny, succulent shrub (0.5 - 2 m in height), consisting of green to blue-green cladodes that are lengthened and flattened (± 230 mm by 100 mm). Spines up to 40 mm are either absent or in groups of one or two (Henderson, 2001). Flowers are large, bowl-shaped, showy, yellow in colour, 50 - 100 mm (Figure 2-3 A) (Henderson, 2001; Bartomeus and Vilà, 2009). The central pistil has four or five lobes, surrounded by numerous stamens (Figure 2-3, A). Flowers produce low volumes of nectar, remaining open for a single day (Spears Jr, 1987). Fruit is in the form of succulent berries, ± 50 mm in length that turn from red to purple (Figure 2-3, B). The outer surface is usually smooth, narrowing towards the base, with clumps of glochids. The inner segment is purple, fleshy, and sour tasting (Rambuda, 2001). Seeds are small, hard and numerous (100 - 200) being viable for up to 15 years (Monteiro *et al*, 2005; Padrón *et al*, 2011; Reinhardt *et al*, 1999; Vilà and Gimeno, 2003).

O. stricta is self-compatible in its native and introduced range (Bartomeus and Vilà, 2009; Spears Jr., 1987). In South Africa *O. stricta* is capable of autonomous self-pollination

(Rambuda and Johnson, 2004), and in Spain, outcrossing was found to increase fruit and seed set (Vilà *et al*, 2009). In Spain, *O. stricta* has successfully co-opted local pollinators, mostly Coleptera and Hymenoptera (Bartomeus and Vilà, 2009; Vilà *et al*, 2009), and *A. mellifera* was found to be the main pollinator of flowers in both South Africa (Rambuda, 2001) and Florida (Spears Jr, 1987). *O. stricta* is also capable of reproducing asexually (Reyes-Agüero *et al*, 2006).

Introduced range

Originally introduced as an ornamental plant in South Africa, *O. stricta* invades Savanna and dry grasslands (Table 2-1) (Henderson, 2001; Rambuda, 2001). In the Kruger National Park, one of the most heavily infested areas of South Africa, *O. stricta* is localized around the Skukuza region (Foxcroft *et al*, 2007, 2008; Lotter and Hoffmann, 1998). It forms dense thickets, that become impenetrable to animals, and is able to outcompete native plant species. The dispersal of seeds is via baboons (*Papio ursinus* (Kerr)) and elephants (*Loxodonta africana* (Blumenbach)) (Foxcroft *et al*, 2007; 2008; Foxcroft and Rejmánek, 2007). Control with *Cactoblastis cactorum* (Berg) and herbicides has limited effect in controlling the spread of this species (Hoffman *et al*, 1998).

O. stricta is also invasive in Australia (Batianoff and Butler, 2002; Stamer *et al*, 1987), the Mediterranean region (Bartomeus and Vilà, 2009; Padrón *et al*, 2011; Vilà *et al*, 2003), which includes Portugal (Monteiro *et al*, 2004) and Italy (Lo Verde and La Mantia, 2011), China (Liu *et al*, 2006; Yan *et al*, 2001), Namibia (Zimmermann *et al*, 2004), New Caledonia, the Solomon Islands, Yemen, Eritrea, Ethiopia and Somalia (Foxcroft and Rejmánek, 2007), and is moderately invasive in southern Tunisia, Libya, Algeria and Morocco (Le Houérou, 1996).

2.1.7 *Passiflora caerulea* L.

Biology

Passiflora caerulea (blue passion fruit, Passifloraceae) originates from South America, occurring from Brazil to Bolivia, Chile, Paraguay, Uruguay and Argentina (Table 2-1) (Bugallo *et al*, 2011; Mediondo and Amela García, 2006). It occurs in dry areas as well as in wetter forests, and especially along forest margins (Mediondo and Amela García, 2006). As an invader, it uses tendrild to attach to its host, climbing over bush clumps, wire fences, along roadsides paths, railways and riverbanks (Figure 2-3, D - F) (Henderson, 2001; Mediondo and Amela García, 2006).

The 5 - 7 lobed leaves are grey- or blue-green in colour, averaging 10 - 20 mm in length (Henderson, 2001; Howell, 1976). Flowers are showy, with the sepals and petals being white to pale pink in colour. The coronal filaments - which are much shorter than the petals - are purple at the base, becoming white in the middle and blue/purple towards the end (Figure 2-3, D) (Henderson, 2001). Anthesis typically occurs in the afternoon, with flowers remaining open for one day (Ruberté-torres and Martin, 1974). The fruit is an ovoid berry (60 mm x 30 mm) with small seeds (± 6 mm x 4 mm). The epicarp of the fruit is green, turning yellow or orange upon maturation while the inner part is red and contains the seeds (Henderson, 2001; Mediondo and Amela García, 2006).

In its native range *P. caerulea* is self-incompatible, and studies have shown only natural pollination experiments yield fruit (Amela García and Hoc, 1997; Morales and Galetto, 2003) but hybridization studies have produced some fruit (Bugallo *et al*, 2011). *Xylocopa* species, long toungued bees and hummingbirds have been recorded as visitors to the flowers of *P. caerulea* in the native range (Amela García and Hoc, 1997; Amela García and Gottsberger, 2009).

Introduced range

P. caerulea is naturalized in New Zealand, several oceanic islands in the Pacific Ocean (Esler, 1988), North America, the United Kingdom (Howell, 1976; Vanderplank, 1997; in Mediondo and Amela García, 2006), occurs in Spain (Dana *et al*, 2001 in Ingale and Hivrale, 2010), East Africa (Lusweti *et al*, 2011) and is considered invasive in the Hawaiian Islands (Space and Flynn, 2002) and South Africa (Table 2-1) (Henderson, 2001). In native Argentina, populations of *P. caerulea* are declining due to urbanisation and unsustainable harvesting of natural populations (Mediondo and Amela García, 2006).

2.1.8 *Pereskia aculeata* Mill.

Biology

Pereskia aculeata (Barbados gooseberry, Cactaceae) is native to eastern South America, the West Indies and Central America (Table 2-1) (Leuenberger, 1986; Paterson *et al*, 2011).

This shrubby to clambering vine has pairs of hooked spines on younger shoots, while older stems have hard, straight spines, 3 - 4 cm long (Henderson, 2001; Paterson *et al*, 2011). Branches are whip-like, extending 2 - 10 m high (Henderson, 2001). Leaves are bright green and glossy, being variable in shape and size (Henderson, 2001; Leuenberger, 1986). Flowers are white, creamy white or yellowish, 3 - 4 cm in diameter, lemon-scented, diurnal, and lasting only one day (Figure 2-4, A) (Henderson, 2001; Leuenberger, 1986; Paterson *et al*, 2009). Stamens are numerous, creamy-white or purple in colour, with exposed anthers having abundant pollen available (Figure 2-4, A) (Boke, 1966; Leuenberger, 1986). Nectaries are present and surround the style base (Leuenberger, 1986). Fruit in the form of succulent berries are green, becoming yellow/orange upon maturation, 1.5 - 2 cm in diameter, and spiny only when immature (Figure 2-4, B) (Henderson, 2001; Leuenberger, 1986; Paterson *et al*, 2009). Seeds are flattened to slightly concave, 6 mm in diameter with 2 - 5 seeds per fruit (Boke, 1966). Fruit are edible (Boke, 1966; Leuenberger, 1986), often being used to make jams (Klein, 1999).

P. aculeata is self incompatible, with self-pollination resulting in fruit being set only occasionally, with seeds being absent or underdeveloped (Leuenberger, 1986). In South Africa, *P. aculeata* is known to reproduce both sexually and asexually (Paterson *et al*, 2009), with abundant fruit being observed in populations in KwaZulu-Natal (Campbell, 1988). Generalized pollination has been suggested as the pollination syndrome for *P. aculeata* in its native range and this is supported by flower morphology (Leuenberger, 1986). Bees, bumblebees and syrphids were observed visiting *P. aculeata* in a greenhouse (Leuenberger, 1986).

Introduced range

P. aculeata was first recorded in South Africa in 1858 in the Botanical Gardens, Cape Town (McGibbon, 1858; Moran and Zimmermann, 1991), and has been present in KwaZulu-Natal since 1881 (Bromilow, 2010). It was listed as being invasive along the coastal regions in KwaZulu-Natal and the Eastern Cape, with frost intolerance preventing its spread inland (Table 2-1) (Campbell, 1988; Paterson *et al*, 2011). Removal of *P. aculeata* by herbicide is ineffective, with biocontrol seen as the best possible method of control, even though successful control has yet to be achieved (Klein, 1999; Moran and Zimmermann, 1991; Paterson *et al*, 2009). New possible biocontrol agents were identified by Paterson *et al*

(2014), and recently the Pereskia stem-wilter (*Catorhintha schaffneri* (Brailovsky and Garcia)) was released on *P. aculeata* in Grahamstown, South Africa.

P. aculeata is naturalized in Australia, (Glaznig *et al*, 2004 in Paterson *et al*, 2014), Hawaii (Paterson *et al*, 2014; Starr *et al*, 2004) and on Carp Island, Palau (Space *et al*, 2009).

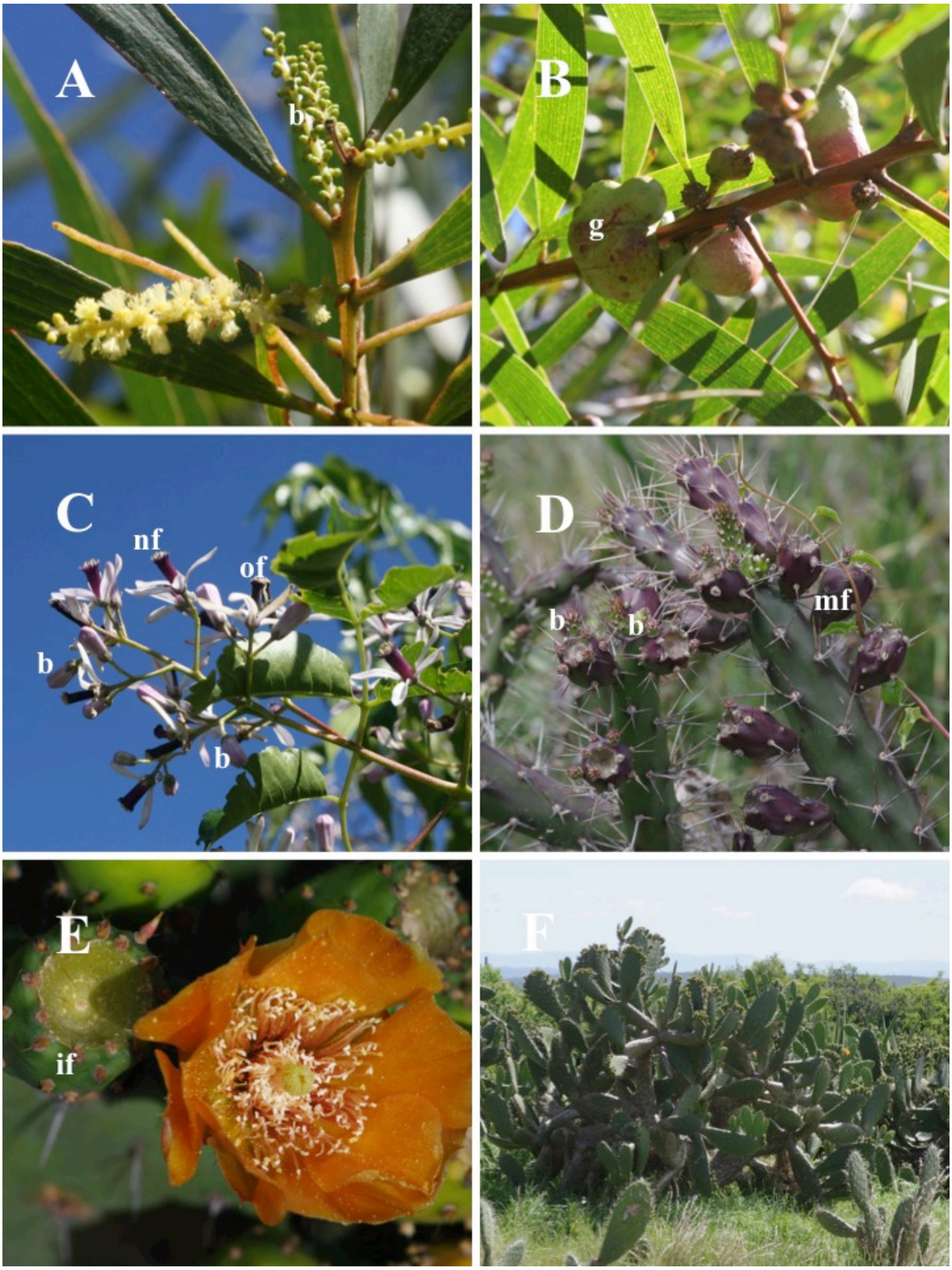


Figure 2-1: A: Flowers and buds (b) of *Acacia longifolia*, B: distinctive galling (g) on *Acacia longifolia* by the biological control agent *Trichilogaster acaciaelongifoliae*, C: fertilized (of) and non-fertilized (nf) flowers of *Melia azedrach*, with buds (b), D: mature fruit (mf) and developing buds (b) of *Opuntia aurantiaca*, E: open flower of *Opuntia ficus-indica* with immature fruit (if), F: dense clump of *Opuntia ficus-indica* at Burnt Kraal, Grahamstown, South Africa.

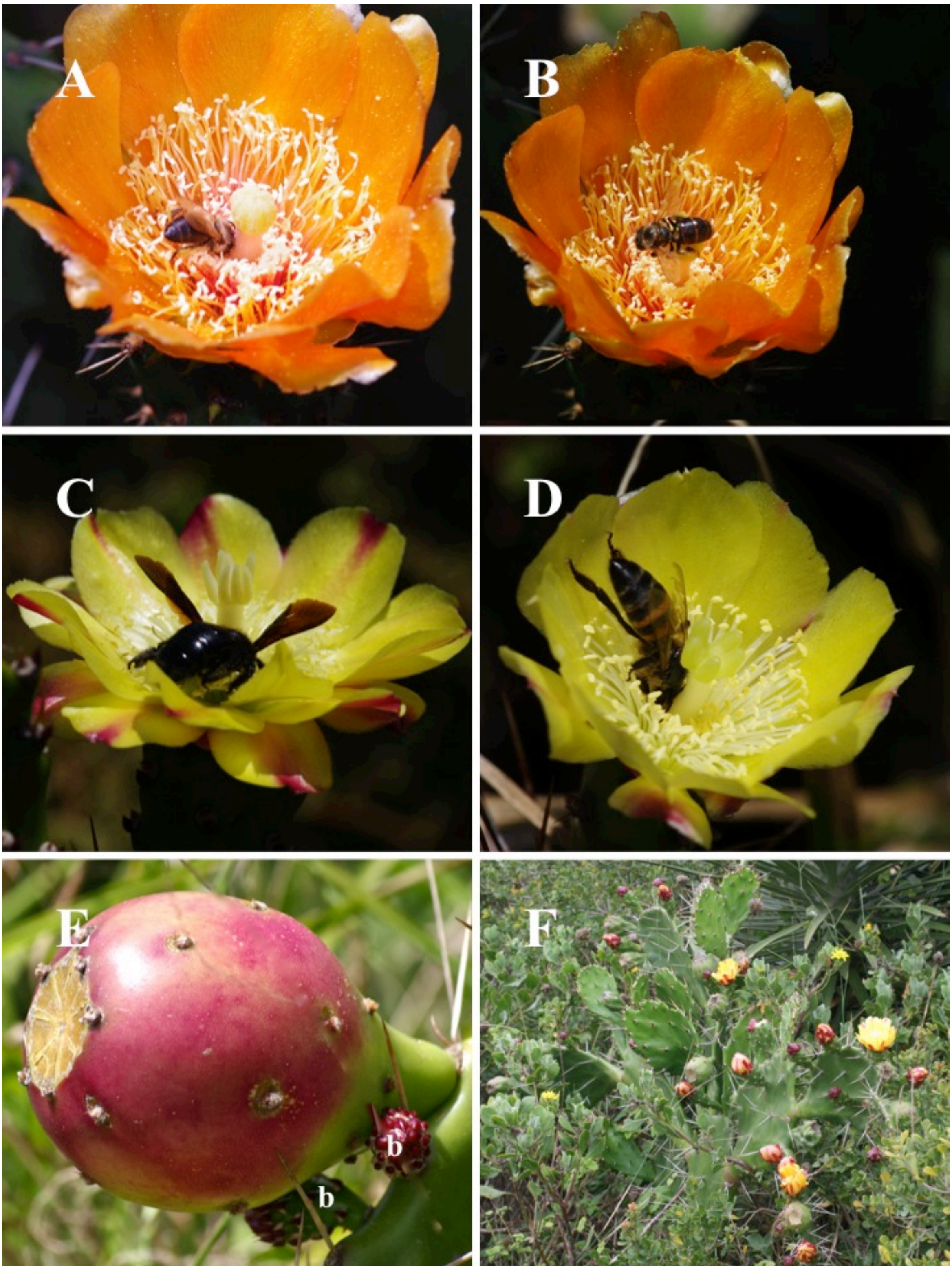


Figure 2-2: A: *Apis mellifera* removing nectar for the flower of *Opuntia ficus-indica*, B: *Apis mellifera* on the stigma of *Opuntia ficus-indica*, C: *Xylocopa* species and D: *Apis mellifera* removing nectar from the flower of *Opuntia monacantha*, E: mature fruit of *Opuntia monacantha*, with developing buds (b), F: *Opuntia stricta* groing amongst native dune vegetation at Port Alfred, South Africa.

Figure 2-3: A: Open flower, and B: mature fruit with developing buds (b), of *Opuntia stricta*, C: example of the mesh bags used for breeding system experiments, D: open flower of *Passiflora caerulea*, with bud (b), E: *Xylocopa* species removing nectar from *Passiflora caerulea*, while pollen is deposited on the thorax, buds (b) are also visible, F: sunbird species removing nectar from *Passiflora caerulea* flower.

Figure 2-4: A: Open flower of *Pereskia aculeata*, B: green immature (if) and orange mature fruit (mf) of *Pereskia aculeata*, C: aborted fruit of *Pereskia aculeata*, D: green immature fruit (if), which later turns black, with flowers and buds (b) of *Solanum chrysotrichum*, E: flowers showing yellow poricidal anthers and bud (b) of *Solanum mauritianum*, F: mature yellow fruit (mf), some partially eaten by birds, and untouched immature green fruits (if) of *Solanum mauritianum*.

2.1.9 *Solanum chrysotrichum* Schltdl.

= *S. hipidium auct. non*. Persoon (Bean, 2004; Nee, 1986; Welman, 2003).

Biology

Solanum chrysotrichum (Giant Devils Fig, Solanaceae) is native to Central America, including southern Mexico, Costa Rica, Guatemala, Nicaragua and Panama (Table 2-1) (Murray, 1988; Taylor, 1963; Welman, 2003). It grows in moist or wet thicket, at an altitude of 1200 - 2500 m (Gentry and Standley, 1974 in Welman, 2003). It is an erect, small evergreen shrub or tree reaching heights of up to 7 m. The leaves are solitary, ovate to elliptical with 7 - 13 lobes. The inflorescence consists of dense cymes of 30 - 40 flowers. Flowers are white, with yellow poricidal anthers (Figure 2-4, D). The fruit is globose (± 10 mm diameter), being green at first, turning orange-yellow to brown when dry (Figure 2-4, D). Seeds are 2 - 3 mm, with 100 - 250 seeds per fruit (Bean, 2004; Symon, 1981; Roa, 1980; Welman, 2003). Flowering and fruiting occurs all-year round (Bean, 2004; Nee, 1986). The tree is distinguished by red/brown pubescence that occurs on the stems, calyx and underside of the leaves. Prickles are also present on the stems, leaves, petioles and juvenile sections (Bean, 2004; Welman, 2003).

S. chrysotrichum (when misidentified as *S. hispidium*) is self-compatible (Baksh and Iqbal, 1979; Whalen and Anderson, 1981), and based on the small flower size, white colour of flowers, the floral reward being pollen, and the poricidal anthers, buzz pollination by sonicating bees is suggested (Albuquerque *et al*, 2006; Buchmann, 1986).

Introduced range

S. chrysotrichum was introduced as an ornamental plant and has become naturalized in subtropical Africa, southern Asia and Australia (Welman, 2003; Bean, 2004, Symon, 1981). In Africa, *S. chrysotrichum* has been collected in West Africa, including Algeria, Guinea and the Democratic Republic of Congo as well as in Zimbabwe, Malawi and southern Africa (Knapp *et al*, 2013; Welman, 2003; White, 1939). *S. chrysotrichum* is naturalized in the Eastern Cape of South Africa from the Albany district to the Libode district (Table 2-1). The oldest record of *S. chrysotrichum* in South Africa is from the Grahamstown area in 1909 (Bromilow, 2010; Welman, 2003). A herbarium specimen from the Cape, in 1882, of *S. chrysotrichum* was found at Kew gardens, was possibly misidentified as *S. hispidium* (Welman, 2003; White, 1939).

2.1.10 *Solanum mauritianum* Scopli.

Biology

Solanum mauritianum (bugweed, Solanaceae) originates from South America, specifically northern Argentina, southern Brazil, Paraguay and Uruguay (Table 2-1) (Henderson, 2001; Olckers, 2008, 2011; Roe, 1972). This small perennial tree or shrub (2 - 10 m) lives for up to 15 years (Henderson, 2001; Olckers, 2011). Adaxial surface of leaves are a dull green colour, while the abaxial surface is covered in white felty hairs. Purple flowers are produced in dense clusters on felty stalks and are produced all-year round (Figure 2-4, E). Fruit forms globose berries (± 10 mm in diameter) in dense clusters that turn from green to yellow upon maturity (Figure 2-4, F) (Henderson, 2001; van Wyk and van Wyk, 2009b). Fruit production starts when trees reach a height of 1.5 m, with approximately 180 seeds being produced per fruit (Jordaan and Downs, 2012; Olckers, 2011; Symon, 1981; Witkowski and Garner, 2008). It is estimated that trees are able to produce up to 200 000 seeds per year upon maturity, with 79% seed viability (Olckers, 2011; Witkowski and Garner, 2008).

S. mauritianum is self-compatible (Rambuda and Johnson, 2004; Roe, 1979) and capable of autonomous self-pollination (Rambuda and Johnson, 2004). It is a generalist species, being visited mostly by bees (Olckers, 2011), such as *A. mellifera* in both South Africa (Rambuda, 2001) and Brazil, and the bee *Melipona obscurior* (Moure) in its native range (Hilgert-Moreira *et al*, 2014). The poricidal anthers suggest buzz pollination by sonicating bees (Buchmann, 1983). *S. mauritianum* is also able to grow vegetatively from root sections when cut or uprooted (Bromilow, 2010; Olckers and Zimmermann, 1991).

Introduced range

In South Africa, *S. mauritanum* is considered one of the worst invaders, possibly being introduced to Africa via the Portuguese trade routes as far back as the 16^{th} century (Olckers and Zimmermann, 1991; Roe, 1979). It was first recorded in Natal in 1862 and declared a noxious weed in 1937. Today, it predominantly occurs along the eastern, higher rainfall region of South Africa (Table 2-1) (Harding, 1938; Olckers, 2004, 2011; Olckers and Zimmermann, 1991). *S. mauritianum* is a major problem including acting as a host for the fruit fly *Ceratitis rosa* (Karsch), which enables large numbers to persist through winter, enabling it to become an economic pest in orchards (Bromilow, 2010; Annecke and Moran, 1982; Ripley and Hepburn, 1930 in Olckers and Zimmermann, 1991). The abundant fruit is favoured by frugivorous birds (Figure 2-4, F), e.g. Rameron pigeons that often prefer the fruit of *S. mauritianum* to that of indigenous plants. The ingested seeds have greater germination rates, are dispersed widely, thus facilitating the invasion (Bromilow, 2010; Jordaan and Downs, 2012; Oatley, 1984; Olckers and Hulley, 1995).

S. mauritianum is naturalized in Mozambique, Swaziland and Zimbabwe, but also further north in western, central and eastern Africa (Olckers, 2003), including Kenya (Copeland and Wharton, 2006). It is considered invasive in New Zealand (McGregor, 1999; Olckers and Borea, 2009), Australia (Florentine *et* al, 2003; Olckers, 2011; van Dyck, 1979), many islands in the Atlantic, Indian and Pacific oceans including La Réunion, Mauritius and Madagscar (Drew and Hooper, 1983; Cronk, 1989; Percy and Cronk, 1996; Olckers, 2011; Roe, 1972; Sherley, 2000; Space and Flynn, 2000) and Australia (Olckers and Zimmermann, 1991).

2.1.11 *Yucca aloifolia* L.

Biology

Yucca is the second largest genus in the family Agavaceae, subfamily Agavoideae, and naturally occurs in the arid parts of Mexico and southern North America (Table 2-1) (Smith *et al*. 2012; Flemming and Holland, 1998). *Yuccas* are divided into two monophyletic sections: Chaenocarpa which have capsular fruit and Sarcocarpa which are the fleshy fruited species (Pellmyr *et al*, 2007), with *Yucca aloifolia* falling into the latter section. *Y. aloifolia* is thought to be an escaped cultivar as it is closely related to *Yucca elephantipes* (Molon) and *Yucca lacandonica* (Gómez Pompa and J. Valdés). *Y. aloifolia* naturally occurs in the northern Caribbean and along the Mexican Gulf and along dunes of southern Atlantic coast (Pellmyr *et al*, 2007) however there is evidence to suggest that *Y. aloifolia* is not native to the southeastern coast of USA as it commonly occurs around human habitation and because it lacks an endemic insect pollinator (Groman and Pellmyr, 2000).

Y. aloifolia is a short, slender tree, approximatly 1 m tall (Figure 2-5, A and B). The flat, rigid leaves have denticulate margins and leaves are produced along the length of the trunk. The inflorescence stalk is < 1 m tall and supports between 150 and 500 flowers. Flowers are a cream/white colour, often tinged green or purple near the base (Figure 2-5, C). Flowers usually open at dusk and flower for 1 - 2 days before closing at dawn (Huth and Pellmyr, 2000). In its native range, this species flowers from mid June to early August (Groman and Pellmyr, 2000; Rentsch, 2013). The dark pruple fleshy fruit is elongated, ± 10 cm in length and 4 cm wide (Figure 2-5, C) (Huth and Pellmyr, 2000; Rentsch, 2013).

The classic Yucca-Yucca Moth interaction was first noticed by George Engelmann in 1872 (Baker, 1986) and today it is understood that most yuccas are obligately dependent on yucca moths for sexual reproduction. The yucca moths carry out a complex pollinator service, whereby moths copulate within a *Yucca* flower, after which the female gathers pollen and flies to another *Yucca* flower. Here she deposits part of the pollen on the stigma of the flower after ovipositing within the ovary (Keeley *et al*, 1984). A female moth may pollinate and oviposite in a single flower multiple times (Addicott, 1986). Within a week the eggs hatch and larvae feed off the developing ovules. When fruit ripens the larva bore a hole through the fruit wall and descend to the ground using a silk thread (Keeley *et al*, 1984). *Y. aloifolia* however, is considered an exception to specilaized yucca - yucca moth pollination syndrome as no specific moth pollinator is known and reproduction in its native range appears to be primarly by vegetative means, through rapid clonal extension and growth from broken off plant parts (Pellmyr, 2003). Honeybees are now believed to be the main pollinators of *Y. aloifolia* in its native range (Rentsch, 2013)

Introduced range

Y. gloriosa and *Y. filamentosa* are grown in southern Africa, however, according to Smith *et al* (2012) only *Y. aloifolia* has become established in the natural vegetation. All three of these *Yucca* species are used as hedging in South Africa and are commonly seen in KwaZulu Natal (Smith *et al*, 2012). The pollination and reproductive biology of *Y. aloifolia* in southern Africa could therefore be important in understanding the potential risk of spread of this species in the region (Table 2-1 shows known current distribution) (Smith *et al*, 2012).

Yuccas are widely cultivated in Central Europe *Yuccas* due to their hardiness (Szabó and Gerzson, 2011). Historical records show that *Y. aloifolia* was moved around by Europeans as far back as the 1500's (Groman and Pellmyr, 2000). A picture in the palace of Versailles depicts a *Yucca* species in Paris as far back as the late 1800s and I observed them on my travels in Switzerland, specifically in the Sankt Gallen Canton (Personal Observation, 2014).

Today, it is found on the islands of Cuba, Jamaica, the Bahamas and Bermuda where populations have become established (Trelease, 1920) and southern Spain, *Y. aloifolia* was introduced as a garden plant and is now naturalized on coastal sand dunes (Asensi *et al*, 2014).

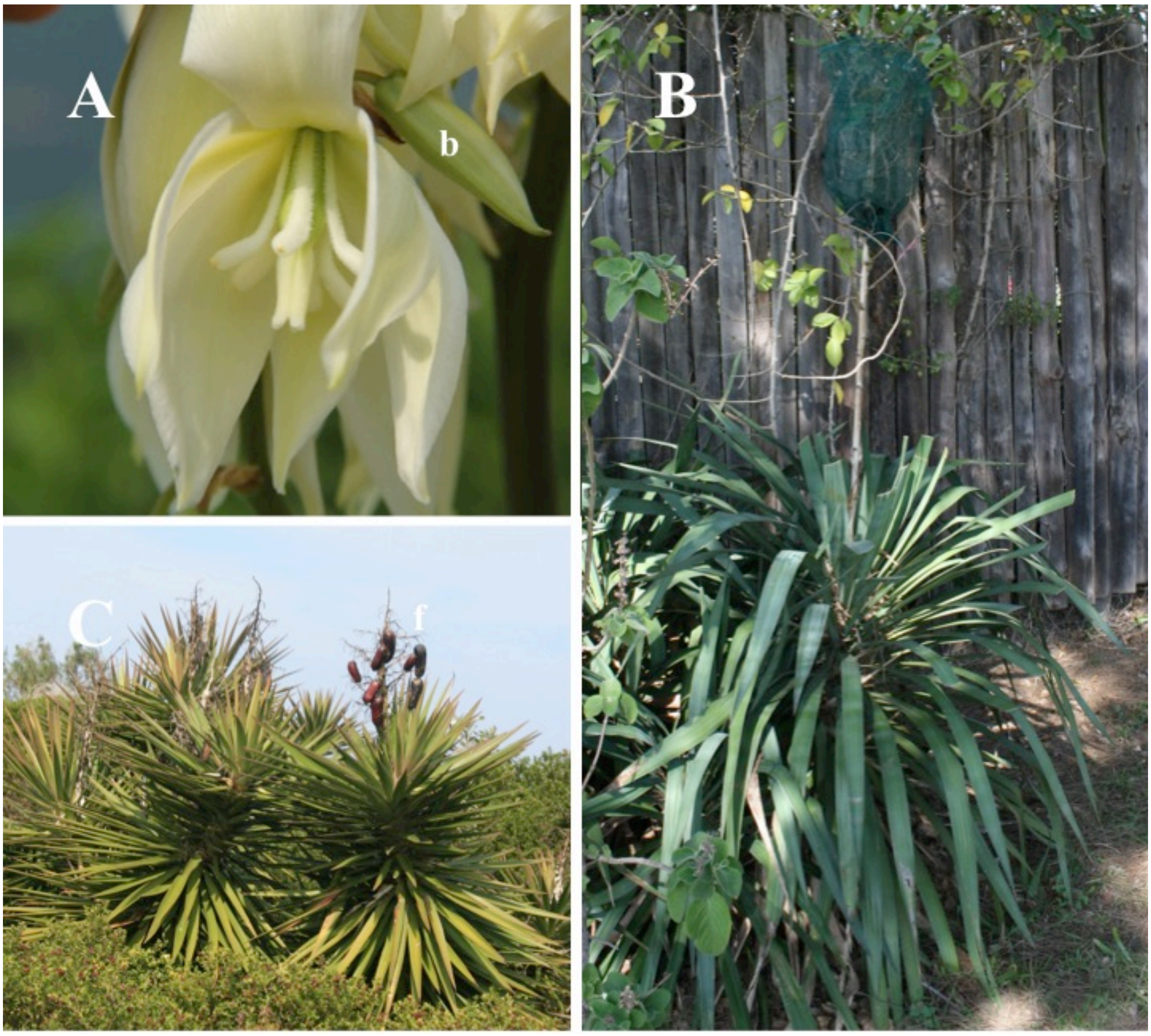


Figure 2-5: A: Open flower of *Yucca aloifolia* showing stigma and anthers, with bud (b), B: shade cloth bag used for pollinator exculsion experiments, Grahamstown, South Africa, C: *Yucca aloifolia* at Port Alfred, South Africa, showing fruit (f).

Chapter 3: Materials and Methods

3.1 Study sites

Study sites were located around the Eastern Cape Province of South Africa. Due to the number of study species it was not always possible to find sufficient population sizes safely situated within the Grahamstown area, thus the surrounding areas of Port Alfred, Kenton-on-sea, Bathurst and Morgan's Bay were also utilized (Table 3-1). Permission to work on road reserve around the Eastern Cape was obtained from the Department of Environmental Affairs and Tourism in Grahamstown.

Table 3-1: Locality data for study species

Study species	Location	GPS co-ordinates
Acacia longifolia	R67 (Stones Hill)	33°20'0.32"S, 26°35'22.14"E
Melia azedarach	Grahamstown	33°18'38.27"S, 26°31'32.14"E
Opuntia aurantiaca	Burnt Kraal	33°16'29.79"S, 26°29'17.96"E
Opuntia ficus-indica	Burnt Kraal R350 (road reserve)	33°16'29.79"S, 26°29'17.96"E 33°14'28.58"S, 26°25'18.60"E
Opuntia monacantha	Burnt Kraal Kariega Game Reserve	33°16'29.79"S, 26°29'17.96"E 33°36'20.81"S, 26°37'27.90"E
Opuntia stricta	Kariega Game Reserve	33°36'20.81"S, 26°37'27.90"E
Passiflora caerulea	Grahamstown Mosslands (N2 road reserve)	33°18'38.27"S, 26°31'32.14"E 33°25'6.53"S, 26°21'29.29"E
Pereskia aculeata	Grahamstown Bathurst	33°18'38.27"S, 26°31'32.14"E 33°29'55.12"S, 26°48'56.52"E
Solanum chrysotrichum	Morgan Bay	32°41'19.18"S, 28°18'10.18"E
Solanum mauritianum	Grahamstown Woest Hill	33°19'2.69"S, 26°30'48.20"E 33°20'58.93"S, 26°33'36.66"E
Yucca aloifolia	Cannon Rocks Grahamstown Kenton-on-sea Port Alfred Standerwick Farm	33°44'50.20"S, 26°32'59.32"E 33°18'38.27"S, 26°31'32.14"E 33°40'46.64"S, 26°39'23.37"E 33°36'16.84"S, 26°53'45.89"E 33°31'7.61"S, 26°54'53.23"E

3.2 Breeding system

Breeding system experiments were conducted on 11 invasive alien plants during 2012, 2013 and 2014. Bags made of fine mosquito netting (Figure 2-3, C) or shade cloth (for *Y aloifolia*) (Figure 2-5, B) were randomly placed on individuals during the bud stage and secured with thick string (or thin wire for *Y. aloifolia*) to exclude pollinators.

Once buds had opened, they were randomly subjected to one of four hand pollination treatments: 1. Manual cross-pollination: upon anthesis, pollen was collected from an individual at least 15 meters away to reduce the likelihood of pollination between related individuals, and placed on the stigma, flowers were then rebagged; 2. Manual self-pollination: upon anthesis, pollen from the same individual was added to the stigma, and the flower bud was rebagged; 3. Autonomous self-pollination: flower buds were left unmanipulated under the bags; 4. Emasculation: before anthesis, the anthers were removed, while the stigma was left unmanipulated, followed by rebagging of the flower bud; 5. At the same time, that treatments were performed, an unbagged flower of the same developmental stage was designated as an open control. Pollen was collected by rubbing a toothpick over the anthers, and then transferring pollen to the stigmas. Each flower was tagged with a string colour corresponding to the treatment conducted. All treatments were conducted on flowers of the same individual, but if too few flowers developed, the nearest neighbour was used. Treated and control flowers were left until fruit maturation. The total number of flowers that set fruit was recorded. The mature fruit was then harvested (unless specified below), weighed and total number of seeds both viable and non-viable (were applicable) contained in each fruit was recorded. Seed set throughout the study was recorded as number of viable seeds produced per fruit from a single flower.

M. azedarach fruit was harvested prior to ripening as the exclusion bags were being interfered with and the trees at risk of being removed. *O. monacantha*, *O. ficus-indica* and *O. stricta* fruits were harvested 3 months after completion of breeding system, allowing sufficient time for seeds to mature. This is a result of bags being interfered with and because fruit can take anywhere between 240 and 428 days to fully mature (see Reyes-Agüero *et al*, 2006). At the laboratory, fruit were weighed and the number of seeds counted (both viable and non-viable where applicable). For *O. aurantiaca* it was difficult to discern individual seeds, so fruit sac was dried in a drier for 3 days before being weighed.

Locality data for all individuals is located in Appendix 2.

3.3 Pollinator Visitation

Pollinators were observed visiting the study species around the Eastern Cape, South Africa. Pollinators were caught while probing for nectar or foraging for pollen on flowers. Insects were placed in individual vials in a cooler box with ice packs and later killed in a freezer. At the laboratory, pollen loads were analysed by rubbing insects with fushin gel, which was then melted on a hot plate and covered with a cover slip. Total number of pollen grains was counted under a compound microscope. Corbiculae of *A. mellifera* was excluded from swab.

3.3.1 *Melia azedarach*

In 2012 no pollinators were observed on *M. azedarach* possibly because of very strong winds. In contrast, numerous pollinator visits were observed in 2013. Pollinator observations took place from 5 am to 7 pm at 2 hour intervals on an inflorescence of approximately 10 cm x 10 cm (± 20 flowers) over 2 consecutive days for 15 minutes. The identity of visiting insect species and the number of flowers visited on the inflorescence was recorded. Number of flowers visited per minute was calculated to determine the visitation rate. Locality data for all insects caught on different species is located in Appendix 3.

3.3.2 *Opuntia* species

Initial observations suggested insects visit a flower for either nectar or pollen. I therefore recorded pollinator foraging preference (nectar or pollen cf. Duffy *et al*, 2014) every 2 hours for 10 minutes, from 8 am to 5 pm for one a flower on an individual plant over 3 non-consecutive days. The identity of visiting insect species and preferred reward was recorded.

3.3.3 Buzz pollination for *Solanum* species

Buzz pollination was expected in *S. chrysotrichum* and *S. mauritianum* on the basis of anther morphology. Buzz pollination occurs when an insect grasps the poricidal anthers tightly with its legs and mandibles and rapidly contracts and relaxes its indirect flight muscles. The flower then vibrates at the same frequency as the vibrating thorax of the bee, releasing pollen onto the bee (Buchmann, 1983, 1986). Inflorescences were harvested from plants, returned to the lab and sonicated with a modified tuning fork vibrating between 120 hz and 240 hz (Appendix 1: Supplementary Video 1). Visible pollen from the anthers was recorded as present or absent for 4 out of 5 anthers on each flower, excluding an anther to account for possible damage or missing anthers. Flowers depleted of pollen were considered ‘visited’, enabling the proportion of flowers already visited by pollinators to be calculated.

3.3.4 Nectar measurements for *Yucca aloifolia*

Abundant nectar was observed in flowers of *Y. aloifolia* and honeybees were reguraly observed visiting flowers, possible in search of a nectar reward. Nectar concentration and volume was measured at 8 am, 12 pm and 5 pm for twenty *Y. aloifolia* individuals. Nectar volume was measured using 5 µl micropipettes for 10 bagged and 10 unbagged flowers. Nectar concentration was recorded using a hand-held refractometer (Atago sucrose refractometer, 0-53% BRIX).

3.4 Pollen limitation

Pollen limitation was investigated for all study species. The degree of pollen limitation was investigated by adding out-crossed pollen onto the stigmas of flowers. Pollen was collected from individuals at least 15 m away to reduce the likelihood of pollination between related individuals and deposited onto one flower per plant. Pollen was added to stigmas using a toothpick or forceps (depending on the species). For the control buds were tagged prior to anthesis. Both treatment and open control were tagged and left unbagged to allow for further natural pollination. The number of individuals and flowers used varied among species and between sites. The treatment and control were conducted on flowers of the same individual where possible, otherwise the nearest viable neighbour was used, along with a second control. The total number of treatments per individual was scored and fruit left to mature. The total number of flowers that set fruit was recorded. The fruit were then harvested, weighed and number of seeds contained in each fruit was recorded. While pollen supplementation experiments can be useful for comparing invasive and non-invasive species (see Knight *et al*, 2005), some limitations do exist. The quality and quantity of pollen recieved may not accurately correspond to natural pollen deposition, inflating estimates, and resource allocation could affect fruit production (Aizen and Harder, 2007; Wesselingh, 2007).

As mentioned previously (section 3.1) *M. azedarach*, *O. monacantha*, *O. ficus-indica* and *O. stricta* fruits were harvested prior to full maturation. At the laboratory fruit was weighed and number of seeds counted (both viable and non-viable were applicable). For *O. aurantiaca*, where it was difficult to discern individual seeds, the fruit sac was dried in a drier for 3 days before being weighed.

3.5 Indices

The following four indices where used to estimate levels of self-compatibility or self-incompatibility in the study species. The degree of pollen limitation was also investigated. These indices are adapted from Lloyd and Schoen (1992), Newstrom and Robertson (2005), Merret (2006), Larson and Barrett (2000) and Riveros *et al* (1998):

Autonomous Selfing Index (ASI) was calculate as follows: ASI = I_A/I_S, where I_A represents the percentage fruit set from autonomous self-pollination (bagged control) and I_S represents the percentage fruit set from the self-pollination treatment. High levels of *autonomous self-pollination* were considered when ASI > 0.75, while ASI < 0.25 indicated *no autonomous self-pollination*.

Pollen Limitation Index (PLI) at the level of fruit set was calculate as follows: PLI = 1 - (I_C/I_{PS}), where I_C is the percentage fruit set for the untreated control and I_{PS} represents the percentage fruit set from pollen supplementation on open, unbagged flowers. A PLI $\leq$ 0 suggests the species is *not pollen limited*, PLI < 0.25 indicates *low levels of pollen limitation*, 0.25 < PLI < 0.75 indicates *medium levels of pollen limitation* and PLI > 0.75 indicates *high levels of pollen limitation*.

Index of Self-Incompatibility (ISI) was calculate as follows: ISI = 1 - (I_S/I_X), where I_S represents the percentage fruit set from self-pollination treatment and I_X represents the percentage fruit set from the cross-pollination treatment. If the ISI > 0.8 the species is classified as *self-incompatible*. Negative values of ISI were set to zero following the methods of Raduski *et al* (2012).

Self-Compatibility Index (SCI) was calculate as follows: SCI = I_S/I_X, where I_S represents the percentage fruit set from the self-pollination treatment and I_X represents the percentage fruit set from the outcross-pollination treatment. *Self-compatibility* was considered when SCI > 0.80, *partial self-compatibility* where 0.20 < SCI < 0.80 and *self-incompatibility* where SCI < 0.20.

The following three indices where used to assign a level of self-compatibility and auto-fertility at the level of seed set to 8 invasive species. Theses indices were adapted from Lloyed and Schoen (1992) and Stout (2007b):

Self-Compatibility Index (SCI) was calculated as follows: SCI = I_S/I_X, where I_S equals mean seed set from self-pollination and I_X equals mean seed set from cross-pollination. Full *self-compatibility* at the seed level was considered where SCI ≥ 1 and *self-incompatibility* where SCI < 0.75. For *Opuntia* species and *Y. aloifolia* species, the proportion of fertile seeds for self-pollination and cross-pollination was used.

Auto-Fertility Index (AFI) was calculate as follows: AFI = I_A/I_X, where I_A equals mean seed set from autonomous self-pollination and I_x equals mean seed set from cross-pollination. The AFI indicates the ability of flowers to produce fertile seeds in the absence of pollinators. The higher the value, the greater the ability to set seed in the absence of pollinators (Escaravage *et al*, 1997). For *Opuntia* species and *Y. aloifolia*, the proportion of mature seeds for each autonomous self-pollination and cross-pollination was used.

Pollen Limitation Index (PLI) at the level of seed set was calculate as follows: Seeds per a flower was calculated where fruit set (as a proportion) was multiplied by average number of mature seeds per flower. The PLI = $1 - (I_C/I_{PS})$, where I_C is the seeds per flower for the untreated control and I_{PS} represents the seeds per flower from pollen supplementation on open, unbagged flowers. A PLI ≤ 0 suggests the species is *not pollen limited*, PLI < 0.25 indicates *low levels of pollen limitation*, $0.25 <$ PLI < 0.75 indicates *medium levels of pollen limitation* and PLI > 0.75 indicates *high levels of pollen limitation*.

3.6 Growth trials, dispersal and asexual root production by fruit

3.6.1 *Opuntia ficus-indica* and *Opuntia aurantiaca*

O. aurantiaca in South Africa is said to be a sterile clone (Archibald, 1936) so growth trials were conducted on the seeds from the breeding system and pollen supplementation experiment conducted in January 2013. Seeds were placed 1 cm below the soil surface layer in seed trays and watered. Following planting, trays were watered twice a week. I planned to quantify percentage seedling emergence but no seeds germinated.

Fruit from the control of *O. ficus-indica* experiment was used to test the viability of black and brown seeds. Twenty fruit were used, with seeds being divided into mature (or black seeds) and immature (or brown) seeds. A total of 20 seeds from each plant were planted in rows 1 cm below the soil surface in large trays. A second experiment consisted of twenty *O. ficus-indica* fruit that were collected from a population at Burnt Kraal, Grahamstown. Mature (black seeds) and immature (brown seeds) from 10 fruit were scattered within a tray filled with soil, while the remaining 10 fruit were placed on the surface of a tray filled with soil. The trays were placed in a greenhouse at the Department of Botany, Rhodes University, and watered twice weekly for the duration of the experiment. After 1, 2 and 3 years the number of seedlings that emerged was recorded and percentage germination calculated.

3.6.2 *Yucca aloifolia*

Growth trials were carried out on *Y. aloifolia* fruit and seeds to investigate whether *Y. aloifolia* is producing 1) viable seeds, 2) whether these seeds could be germinating in natural environments and 3) whether seeds in partly eaten fruit as dispersed by birds could germinate.

The first trial involved collecting fruit from the Grahamstown area. Seeds were planted approximately 1 cm below the surface, in rows with 6 black seeds per a row in one tray. In the second tray black seeds were randomly scattered on the surface, with none being planted in the soil. No white infertile seeds were used. Trays were maintained in a greenhouse in the Botany Department at Rhodes University where they were lightly watered twice a week. Number of seedlings that emerged after 1 year was recorded and the percentage seeds that germinated calculated.

For the second growth trial, *Y. aloifolia* fruits were collected from Grahamstown, Port Alfred, Kenton-on-sea (and Kenton Marina), Bushman’s River and Cannon Rocks. A plot on Standerwick farm, Port Alfred (33°31'7.50"S, 26°54'53.59"E), was cleared for the germination trial. Two treatments were conducted, with the trial commencing in September 2013. Entire fruits were lightly slit in order to mimic damage observed by feeding birds were placed on the ground, with the slit facing downwards. The second treatment involved digging a small hole, no deeper than 2 cm and placing all the seeds from a single fruit in the ground. These seeds were covered with a thin layer of topsoil. All the fruit and seeds were watered once and left. The number of seedlings germinating for each treatment was recorded on 31 March 2014, 19 August 2014 and 31 October 2014. The number of seedlings germinating were divided by average number of seeds per fruit to calculate germination rate.

3.6.3 Rooting of fruit in *Opuntia* species

The development of roots was observed after harvesting of the fruit of some *Opuntia* species and I hypothesised that the fruit may serve as asexual propagules. Root development on fruits was recorded and the percentage rooting among all the treatments calculated.

3.7 Data Analysis

3.7.1 *Fruit set*

The percentage of treated flowers setting fruit was calculated. Percentage fruit set was calculated by dividing total number of harvested fruit per trreatment by the total number of flowers pollinated for the treatment and multiplying this by 100.

The number of flowers pollinated and total number of fruit harvested i.e. fruit set was analysed using a GLM, with binomial distribution, and by changing the reference treatment to determine which treatements differed from one another.

3.7.2 *Fruit weight*

Breeding system data for 8 invasive species was analysed by conducting a Shapiro-Wilkes test to test for normality. Normally distributed data was fitted with a Linear Model (LM) to see if fruit weight differed between the control and four treatments namely cross-pollination, self-pollination, autonomous self-pollination and emasculation. Data that was not normally distributed was fitted with a Generalized Linear Model (GLM) with Poisson error distribution or Gamma error distribution with identity link function. If the overall model was significantly different, I conducted an Analysis of Variance (ANOVA) followed by Tukey’s HSD post hoc test to test for significant differences between the treatments.

Pollen limitation data was analysed using Shapiro-Wilkes test for normality, and if the assumptions were not met then data was log transformed. Normally distributed data was analysed using a LM. A GLM, with quasipoisson error and log link function (to account for over dispersion), were used were necessary.

3.7.3 *Number of seeds*

Breeding system data for 8 invasive species was analysed using a Shapiro-Wilkes test followed by a GLM with 1) Guassian error distribution, 2) Poisson error distribution, or 3) Quasipoisson error distribution (to account for over dispersion), with log link function. This was to see if the number of seeds differed between the control and four treatments namely cross-pollination, self-pollination, autonomous self-pollination and emasculation. For *O. aurantiaca* seed weight was analysed against the different treatments and control using a GLM with Gamma error distribution and identity link function. If the overall model was significantly different, I conducted an Analysis of Variance (ANOVA) followed by Tukey's HSD post hoc test (with package Multcomp) to test for significant differences between the treatments.

Pollen limitation data was analysed using a Shapiro-Wilkes test to test for normality. A GLM with either 1) Poisson distribution, or 2) Quasipoisson distribution with log link, or 3) Guassian distribution with identity link function.

3.7.4 *Nectar/Pollen preference*

The preference of either nectar or pollen by bees for *Opuntia* species was analysed using a Pearson's Chi squared test was to see if there was any differences in reward choice between the four species.

3.7.5 *Buzz mimicry*

A GLM, with poisson error was used to compare the proportion of anthers (out of four) producing explosive pollen when sonicated for two species, *S. chrysotrichum* and *S. mauritianum*.

All analyses were conducted using R 3.1.2 (R Development Core Team, 2014).

Chapter 4: Results

4.1 Breeding system and Indices

4.1.1 *Acacia longifolia*

A simplified breeding system was conducted on *Acacia longifolia* in 2013 but no fruit was set. In 2014 buds were bagged and a corresponding open control marked. A significant difference was found between the treatments ($F_{(4,98)} = 15.18$, $p < 0.001$) (Figure 4-1, A), with the control treatment being significatly greater than autonomous self-pollination, emasculation, self-pollination and cross-pollination. Fruit set for the open control was 79%, while the bagged flowers, testing for autonomous self-pollination set 15% fruit (Figure 4-1, A).

4.1.2 *Melia azedarach*

The percentage fruit set was significantly different, with outcrossing treatment and control having a significantly greater percentage fruit set, compared to all other treatments ($F_{(4,115)} = 36.59$, $p < 0.001$) (Figure 4-1, B). Cross pollination yielded 75% fruit set, self-pollination yielded 4% fruit set, autonomous self-pollination yielded 17% and the open controls 88% fruit set (Figure 4-1, B). This was all significantly different from the emasculation treatment, which set no fruit (Figure 4-1, B). There was no overall significant difference in average fruit weight between the treatments and open control ($F_{(3,40)} = 0.3$, $p = 0.814$), except for the emasculation treatment (Figure 4-1, B). There was also no significant difference in the average number of seeds per fruit between treatments and the control ($F_{(3.40)} = 3.8$, $p = 0.284$) (Figure 4-1, B). For fruit set, the Self-Compatibility Index (SCI) indicates this species is self-incompatible and the Autonomous Selfing Index (ASI) shows this species to be capable of autonomous self-pollination (Table 4-1). At the level of seed set, the Self-Compatibility Index (SCI) suggests this species is self-incompatible and the Auto-Fertility Index (AFI) indicates a moderate capacity to set seed in the absence of pollinators (Table 4-2).

4.1.3 *Opuntia aurantiaca*

There was no significant difference in fruit set between the treatments and open control ($F_{(4,120)} = 0.17$, $p = 0.954$) (Figure 4-1, C). There was also no significant difference in average fruit weight between the treatments and control ($F_{(4,120)} = 1.60$, $p = 0.182$) (Figure 4-1, C). There was however a significant difference in the average seed weight per fruit ($F_{(4,120)} = 2.6$, $p = 0.038$) (Figure 4-1, C) although none of the seeds developed into mature black seeds. The indices show this species to be self-compatible and the ASI shows this species is capable of autonomous self-pollination (Table 4-1). At the level of seed set, the SCI suggests this species is self-incompatible and the AFI indicates a low capacity to set seed in the absence of pollinators (Table 4-2).

4.1.4 *Opuntia ficus-indica*

There was a significant difference in fruit set ($F_{(4,117)} = 2.85$, $p = 0.027$), (Figure 4-2, D), with self-pollination having signficantly less fruit set compared to the cross-pollination treatment and control. There was however a significant difference between the treatments and open control for average fruit weight ($F_{(4,110)} = 17.2$, $p < 0.001$) and the average number of mature seeds per fruit ($F_{(4,110)} = 8.0$, $p < 0.001$) (Figure 4-2, D). Cross-pollination had 67% of the total number of seeds being viable, self-pollination had 33% seed viability, autonomous self-pollination had 4% seed viability, emasculation had 20% seed viability, while the open control had 39% of the total number of seeds maturing. The maximum number of seeds in a fruit was 1064. This suggests this species is self-compatible and this is supported by the SCI (Table 4-1). The results also show *O. ficus-indica* to be capable of reproducing via agamospermy, with the ASI showing high levels of autonomous self-pollination (Table 4-1). At the level of seed set, the SCI suggests this species is self-incompatible and the AFI indicates a high capacity to set mature seeds in the absence of pollinators (Table 4-2).

4.1.5 *Opuntia monacantha*

There was no significant difference in fruit set ($F_{(4,100)} = 1.14$, $p = 0.342$) and average fruit weight ($F_{(4,88)} = 0.7$, $p = 0.565$) between the treatments and open control for *O. monacantha* (Figure 4-2, E). There was also no significant difference in average number of mature seeds per fruit ($F_{(4,88)} = 1.1$, $p = 0.377$) (Figure 4-2, E). The average number of mature seeds for cross-pollination was 2%, 4% for self-pollination, 4% for autonomous self-pollination, 10% for emasculation and 0% for the open control. The maximum number of seeds per fruit was 190 and the overall average number of seeds per fruit was 48. This suggests *O. monacantha* is self-compatible and capable of reproducing via agamospermy. This is supported by the SCI of 0.96, which suggests this species is self-compatible, while the ASI of 1.04 supports this species being capable of autonomous self-pollination (Table 4-1). At the level of seed set, the SCI of 3.03 suggests this species is fully self-compatible and the AFI of 1.01 indicates a high capacity to set mature seeds in the absence of pollinators (Table 4-2).

4.1.6 *Opuntia stricta*

There is no significant difference in fruit set between the treatments and control for *O. stricta* ($F_{(4,131)} = 0.24$, $p = 0.916$) (Figure 4-2, F). There is however a significant difference in average fruit weight ($F_{(4,127)} = 12.6$, $p < 0.001$) and average number of mature seeds per fruit ($F_{(4,127)} = 13.8$, $p < 0.001$) (Figure 4-2, F). Average fruit weight for cross-pollination and self-pollination treatments were significantly different from autonomous self-pollination, emasculation and the open control (Figure 4-2, F). The cross-pollination treatment set a mean of 11 mature seeds per fruit and 21 immature seeds, with 66% of the total seed set maturing into viable black seeds. Average seed set for self-pollination was 46 mature seeds and 13 immature seeds per fruit, with 78% of the total seed set maturing. Autonomous self-pollination yielded 20 mature seeds and 36 immature seeds on average per fruit, with 35% of the total number of seeds maturing, while the emasculation treatment set 12 mature seeds and 38 immature seeds on average per fruit, with 24% of the total number of seeds maturing. The open control set 9 mature seeds and 32 immature seeds on average per fruit, with 21% of the total number of seeds maturing. The maximum number of seeds per fruit was 131, while the average number of seeds per fruit was 53. The SCI suggest this species is self-compatible, and the ASI suggests this species is capable of autonomous self-pollination (Table 4-1). At the level of seed set, the SCI suggests this species is fully self-compatible and the AFI indicates a high capacity to set mature seeds in the absence of pollinators (Table 4-2).

4.1.7 *Passiflora caerulea*

An initial breeding system experiment of *P. caerulea* did not yield any fruit in 2012 and it was realised that stigmas are only viable in the afternoon of anthesis. In 2013 and 2014 the breeding system was conducted on freshly opened flowers and fruit developed, but unidentified lepidopteran larvae ate them before they could be harvested to quantify fruit and seed quality. In terms of fruit set there was a significant difference between cross-pollination and self-pollination, with 11% fruit set in the cross-pollination treatment, 3% in the self-pollination treatment, and the open control yielded 16% fruit ($F_{(4,234)} = 3.10$, $p = 0.016$) (Figure 4-1, G). Autonomous self-pollination and emasculation treatments did not set fruit suggesting this species is only partially capable of autonmous self-pollination (Figure 4-1, G). According to the ISI this species is self-incompatible and the ASI indicates this species in not capable of autonomous self-pollination (Table 4-1).

4.1.8 *Pereskia aculeata*

Breeding systems were carried out on *P. aculeata* in 2013 and 2014 but only 6 fruit were set among all the treatments over the two years. Even cross-pollination between a population in Bathurst and Grahamstown did not yield any fruit (Figure 4-1, H), yet mature, yellow fruit were occasionally observed in populations. Overall there was no significant difference in fruit set between the treatments and control ($F_{(6,437)} = 1.19$, $p = 0.312$) (Figure 4-1, H). Cross-pollination set 1 fruit, autonomous self-pollination set 4 fruit and the open control set 1 fruit.

4.1.9 *Solanum chrysotrichum*

There is a significant difference in fruit set between the emasulation treatment and outcrossing, selfing, autonomous self-pollination and the control for *S. chrysotrichum* ($F_{(4,134)} = 11.13$, $p < 0.001$) (Figure 4-3, I), with 61% fruit set for cross-pollination, 73% fruit set for the self-pollination, 38% for autonomous self-pollination and 77% for the open control. There was no fruit set in the emasculation treatment. There was no significant difference in the average fruit weight ($F_{(3,65)} = 0.2$, $p = 0.923$) and average number of seeds per fruit ($F_{(3,65)} = 0.9$, $p = 0.467$) (Figure 4-3, I) for the autonomous self-pollination, cross- and self-pollination treatments and open control. The maximum number of seeds in a fruit was 406 and the overall average number of seeds per fruit was 222. Self-compatibility in *S. chrystotrichum* is supported by the SCI, while the ASI suggests moderate levels of autonomous self-pollination (Table 4-1). At the level of seed set, the SCI suggests this species is self-compatible and the AFI indicates a high capacity to set seed in the absence of pollinators (Table 4-2).

4.1.10 *Solanum mauritianum*

There is a significant difference in the fruit set of *S. mauritianum* ($F_{(4,81)} = 8.49$, $p < 0.001$), between the emasculation treatment and the remaining treatments and control (Figure 4-3, J).

There is also a significant difference in average fruit weight ($F_{(4,45)} = 5.4$, $p < 0.001$) and average number of seeds per fruit ($F_{(4,45)} = 4.2$, $p = 0.005$) (Figure 4-3, J) for the autonomous self-pollination, cross- and self-pollination treatments and open control. The maximum number of seeds found in a fruit was 347 and the average number of seeds per fruit was 173. *S. mauritianum* is self-compatible based on the SCI and capable of autonomous self-pollination based on the ASI (Table 4-1). At the level of seed set, the SCI suggests this species is self-compatible and the AFI indicates a moderate capacity to set seed in the absence of pollinators (Table 4-2).

4.1.11 *Yucca aloifolia*

There is a no significant difference in fruit set for *Y. aloifolia* ($F_{(4,158)} = 0.76$, $p = 0.551$) (Figure 4-3, K). No fruit was set for the emasculation treatment. There was a significant difference in mean fruit weight ($F_{(3,17)} = 7.1$, $p = 0.003$) and average number of mature seeds per fruit ($F_{(3,17)} = 5.8$, $p = 0.007$) (Figure 4-3, K). Cross-pollination set an average of 133 mature seeds and 11 immature seeds per fruit, with 92% of the total number of seeds maturing into viable black seeds. Self-pollination yielded an average of 160 mature seeds and 12 immature seeds per fruit, with 31% of the total number of seeds maturing. Autonomous self-pollination yielded an average of 70 mature seeds and 17 immature seeds per fruit, with 11% of the total number of seeds per fruit maturing. For the open control, an average of 41 seeds per fruit matured, with 6% of the total number of maturing. The maximum number of seeds in a fruit was 186 and the overall average number of seeds per fruit was 97. This suggests *Y. aloifolia* is partially self-compatible and this is supported by the SCI and the ASI (Table 4-1). At the level of seed set, the SCI suggests this species is self-incompatible and the AFI indicates a low capacity to set seed in the absence of pollinators (Table 4-2).

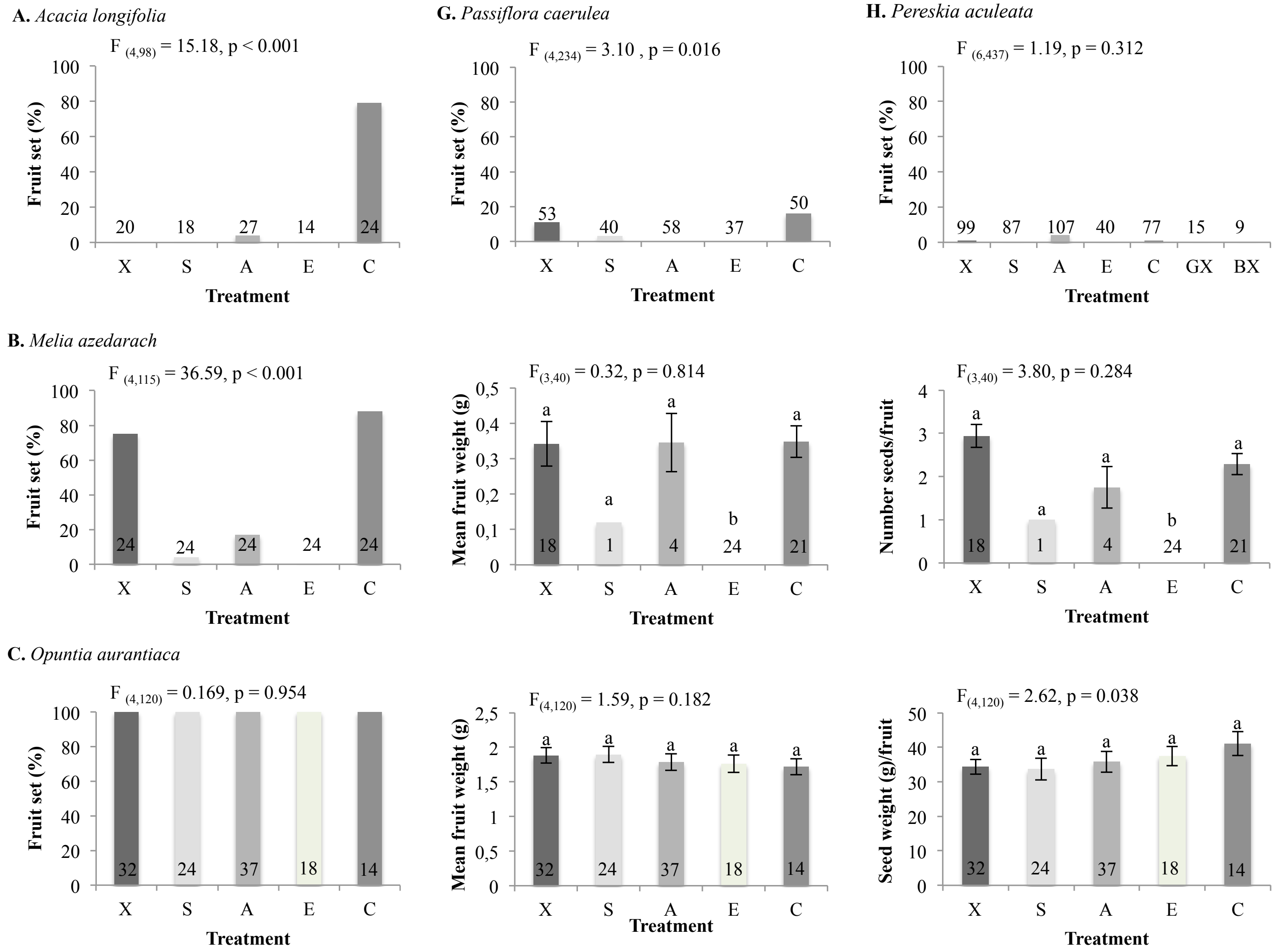
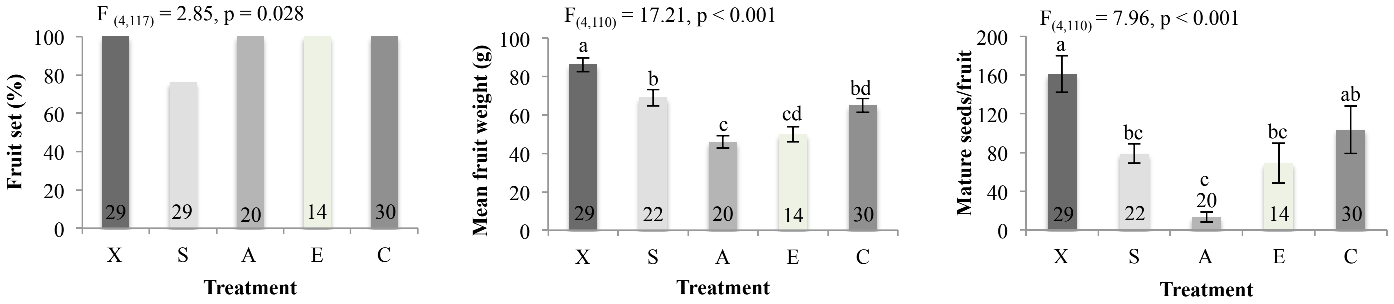
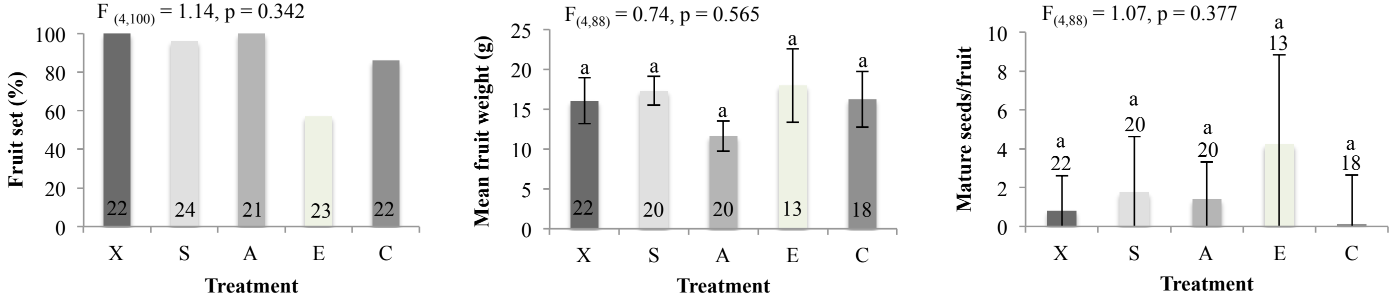


Figure 4-1: Breeding system of 5 invasive species showing percentage fruit set, average fruit weight per treatment and average number of seeds per fruit, average seed weight (for *Opuntia aurantiaca*) or average number of mature seeds per fruit were applicable. X: cross-pollination after bagging, S: self-pollination after bagging, A: bagging with no manipulation, E: emasculation of anthers on bagged flowers, GX: pollen from Grahamstown flowers used to pollinate Bathurst flowers, BX: pollen from Bathurst flowers used to pollinate Grahamstown flowers, C: open control. Bars represent standard error. Sample size is displayed as numbers on graph. Letters above graphs show where significant differences lie.

D. *Opuntia ficus-indica*



E. *Opuntia monacantha*



F. *Opuntia stricta*

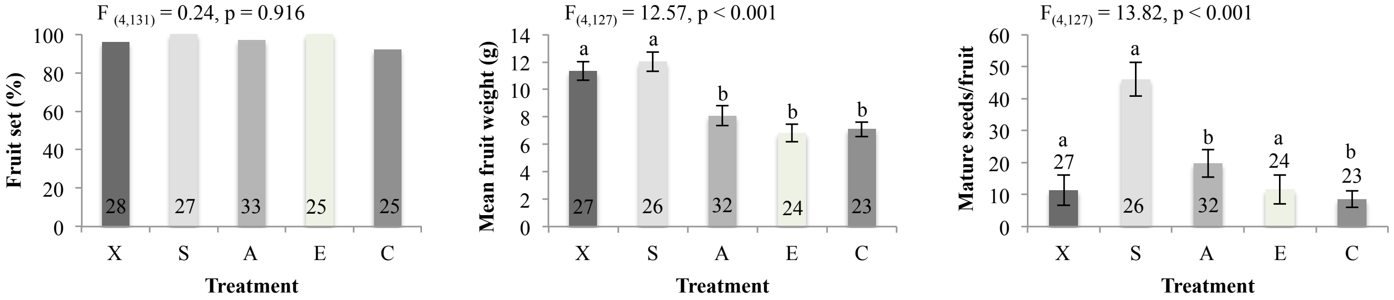


Figure 4-2: Breeding system of 3 invasive species, showing percentage fruit set, average fruit weight per treatment and average number of seeds per fruit or average number of mature seeds per fruit were applicable. X: cross-pollination after bagging, S: self-pollination after bagging, A: bagging with no manipulation, E: emasculation of anthers on bagged flowers, C: open control. Bars represent standard error. Sample size is displayed as numbers on graph. Letters above graphs show where significant differences lie.

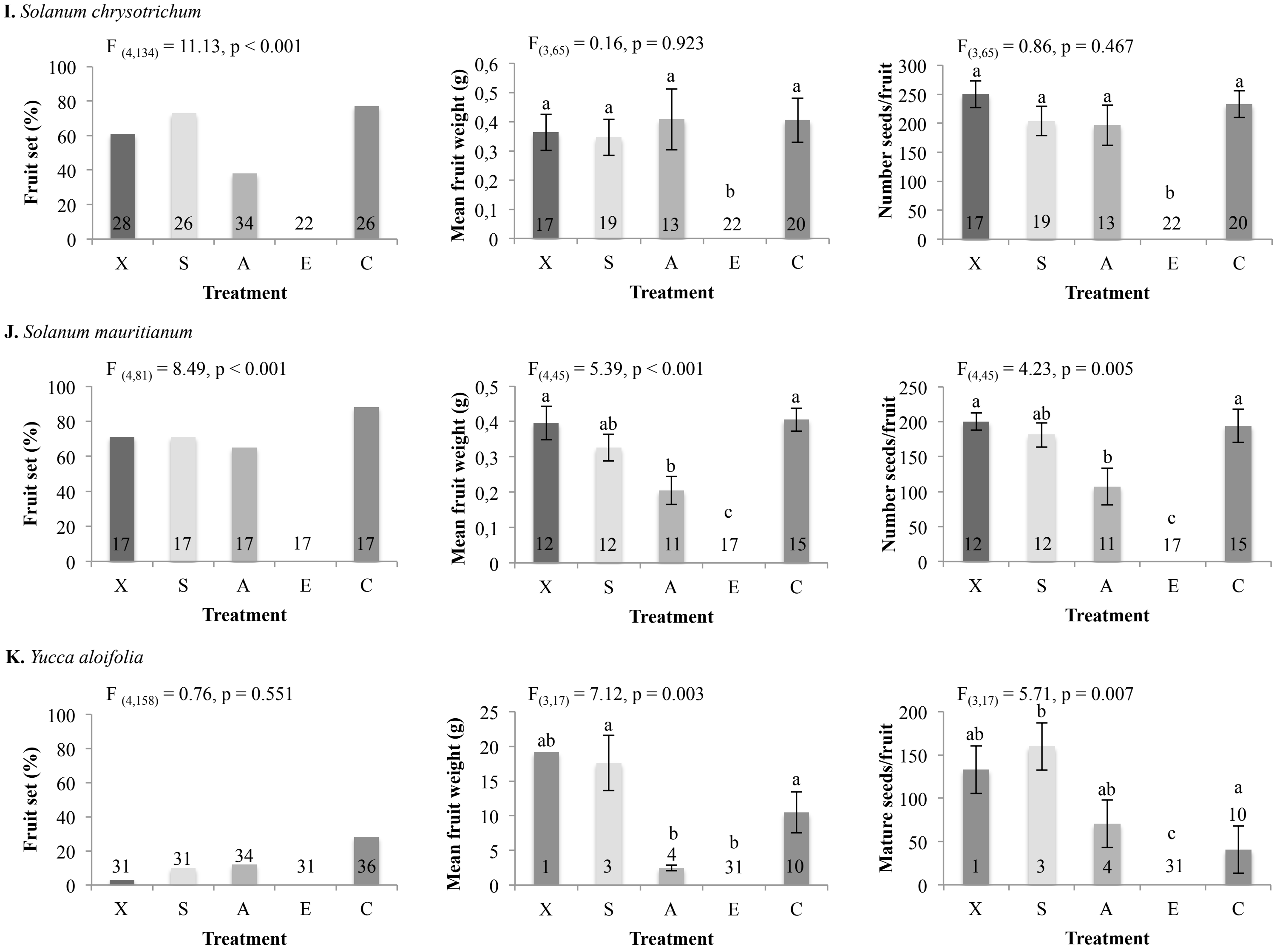


Figure 4-3: Breeding system of 3 invasive species, showing percentage fruit set, average fruit weight per treatment and average number of seeds per fruit or average number of mature seeds per fruit were applicable. X: cross-pollination after bagging, S: self-pollination after bagging, A: bagging with no manipulation, E: emasculation of anthers on bagged flowers, C: open control. Bars represent standard error. Sample size is displayed as numbers on graph. Letters above graphs show where significant differences lie.

Table 4-1: Using indices to assign a compatibility rating at the level of fruit set for 11 invasive plant species. ASI: Autonomous Selfing Index, where ASI > 0.75 is *capable* of autonomous self-pollination and ASI < 0.25 is *not capable* of autonomous self-pollination. ISI: Index of Self-Incompatibility, where ISI > 0.8 equals *self-incompatible*. SCI: Self-Compatibility Index where SCI > 0.80 equals *self-compatible*, 0.20 < SCI <0.80 equals *partial self-compatibility* and SCI < 0.20 equals *self-incompatibility*. A: autonomous self-pollination, SI: self-incompatibility, SC: self-compatibility. A dash (-) represents insufficient data to allow for analysis.

Plant Species	**ASI**		**ISI**		**SCI**	
	Value	**Rating**	**Value**	**Rating**	**Value**	**Rating**
Acacia longifolia	-	-	-	-	-	-
Melia azedarach	4	A	0.94	SI	0.06	SI
Opuntia aurantiaca	1	A	0	Not SI	1	SC
Opuntia ficus-indica	1	A	0	Not SI	1	SC
Opuntia monacantha	1.04	A	0.04	SI	0.96	SC
Opuntia stricta	0.97	A	0	Not SI	1.04	SC
Passiflora caerulea	0	Not A	0.78	SI	-	-
Pereskia aculeata	-	-	0	Not SI	-	-
Solanum chrysotrichum	0.52	A	0	Not SI	1.20	SC
Solanum mauritianum	0.92	A	0	Not SI	1	SC
Yucca aloifolia	1.22	A	0	Not SI	3	SC

Table 4-2: Using indices to assign a compatibility and auto-fertilization rating to 8 invasive species at the level of seed set. Self-Compatibility Index (SCI): where SCI ≥ 1 equals *self-compatibility* and SCI < 0.75 equals *self-incompatibility*. Auto-Fertility Index (AFI) is the ability of flowers to set fruit in the absence of pollinators, with the higher the value, the greater the ability. SI: self-incompatible, SC: self-compatible. Insufficient data was available for *A. longifolia*, *P. caerulea* and *P. aculeata* in order to conduct anaylsis.

Plant Species	**SCI**		**AFI**	
	Value	**Rating**	**Value**	**Rating**
Melia azedarach	0.33	SI	0.69	Moderate
Opuntia aurantiaca	0.00	SI	0.00	Low
Opuntia ficus-indica	0.63	SI	0.83	High
Opuntia monacantha	3.03	Fully SC	1.01	High
Opuntia stricta	4.35	Fully SC	1.61	High
Solanum chrysotrichum	0.82	SC	0.79	High
Solanum mauritianum	0.91	SC	0.54	Moderate
Yucca aloifolia	0.34	SI	0.13	Low

4.2 Pollinators

Bees were the most common visitors to invasive plant species in the Eastern Cape, with honeybees (*Apis mellifera* (Linnaeus)) being the most commonly caught visitors to 9 of the 11 species (Table 4-3).

4.2.1 *Acacia longifolia*

A total of four taxa visited *A. longifolia* (Table 4-3). Honeybees were the main visitors to this species (84 %) but also had the largest pollen loads ($\bar{x}$ = 77 pollen grains, n = 21) (Table 4-3). *Asarkina africana* (Bezzi) ($\bar{x}$ = 3 pollen grains, n = 2) and the *Allopdape* species (3 and 23 pollen grains) contibute little to the pollination of *A. longifolia* although samples sizes are small (Table 4-3). Pollinators foraged most actively for pollen along flower clusters between 11h00 and 13h00. No nectar could be detected in these flowers.

4.2.2 *Melia azedrach*

A total of 10 different taxa visited this species (Table 4-3).The visitation rate for this species remained constant throughout the day with peaks at 7h00 and 12h00 (Figure 4-4). *A. mellifera* was the most common visitor constituting 81.9% of visits by pollinators (Figure 4-5) and carrying the greatest pollen loads ($\bar{x}$ = 664 grains, n = 16) (Table 4-3). *Xylocopa* species constituted 18% of visits but carried a larger number of pollen grains (Table 4-3). *Xylocopa flavicollis* (De Geer) carried 976 pollen grains (n = 11) on average, while a single *Xylocopa caffra* (L.) carried 2716 pollen grains suggesting they contribute meaningfully to pollination of this species, although their size means they may not always make direct contact with the stigmas located within the small flowers (Table 4-3). Other insects from the Chrysomelidae, Cucujoidea, Nitidulidae (cf), Tachinidae, Dpitera, Scarabaeidae and Apidea were caught visiting *M. azedarach* and all accumulated relatively small pollen loads suggesting a relatively small contribution to pollination (Table 4-3). The remaining 0.1% of recorded visitations to *M. azedarach* flowers were single visits from an *Allodapula* species, butterfly and hawkmoth (Figure 4-4). The single hawkmoth observation occurred at 7 pm, with 12 flowers visited on a single observed clump within 5 minutes (Figure 4-4, Figure 4-5). All Lepidoptera visits occurred in the afternoon. A glucose test revealed very small quantities of a low concentration nectar in *M. azedarach* suggesting high visitation rates may deplete the standing crop of nectar or that many pollinators are collecting pollen as the main reward.

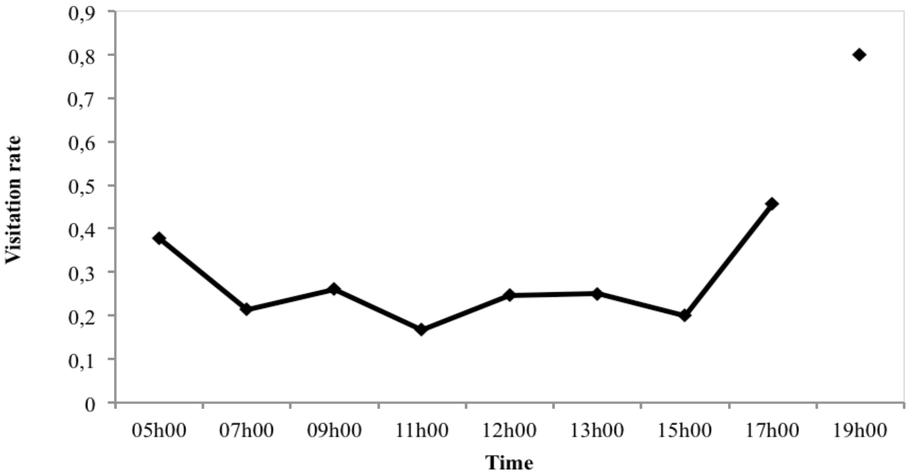


Figure 4-4: Number of flowers visited per minute by pollinators to *Melia azedarach* over a two-day period. The outlier represents a single visit by a hawkmoth.

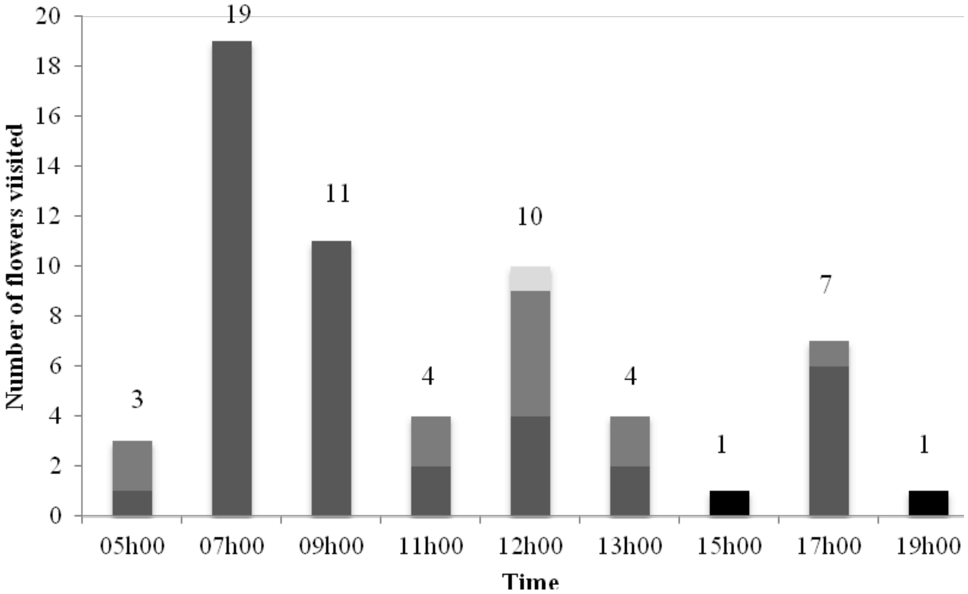


Figure 4-5: Visitation to *Melia azedarach* by pollinators over a 14 hr period. Black: Lepidoptera, dark grey: honeybees, medium grey: carpenter bees and light grey: *Allodapula* species. Numbers above bars represent total sample size in each period.

4.2.3 *Opuntia aurantiaca*

Three species were observed visiting *O. aurantiaca* (Table 4-3). Honeybees were the most common insects caught and observed on this species, suggesting they contribute most to pollination based on pollen loads (x̄ = 212 pollen grains, n = 24) compared with the single *Anthophora (Heliophila) wartmanni* (Friese), which only had 24 pollen grains (Table 4-3). *Xylocopa* species were recorded feeding on nectar on two of the three observation days and always around midday, but it was not possible to capture any of these bees. Flowers are positively thigmotrophic and when bees land on the flowers they walk over anthers, the anthers are triggered to move towards the stigma. Bees landing on *O. aurantica* come into contact with both stigmas and anthers as they move around the open, bowl shaped flowers.

4.2.4 *Opuntia ficus-indica*

Honeybees were the only pollinators caught and observed on this species, with the number of pollen grains per insects ranging from 1 to 485 (x̄ = 141 pollen grains, n = 28) (Figure 2-2, A and B) (Table 4-3). Similar to *O. aurantiaca* flowers are positively thigmotrophic (See attached link for a video of thigmotrophism in *Opuntia ficus-indica* (Appendix 1: Supplementary Video 2) and when honeybees come into contact the open, bowl shaped flowers they access both stigams and anthers as they move around the flower (Figure 2-2, A and B).

4.2.5 *Opuntia monacantha*

Carpenter bees were observed visiting flowers and appear to only be feeding on nectar of *O. monacantha* on all three observation days (between 11h00 and 15h00) and see Figure 2-2 (C). In contrast, honeybees varied in their reward choice throughout the day, choosing both pollen and nectar. Figure 2-2 (D) shows a honeybee removing nectar from a flower. Honeybees had high pollen loads ranging from 156 to 298 pollen grains (x̄ = 233 pollen grains, n = 28) (Table 4-3). A single individual of a species of *Allodape* with 179 pollen grains was also caught (Table 4-3). As mentioned for previous *Opuntia'*s, the flowers respond to the stimulus of visiting insects, and the anthers move rapidly (± 3 seconds) towards stigams. Bees freely move around the open, bowl shaped flowers, coming into contact with both anthers and stigmas.

4.2.6 *Opuntia stricta*

A total of five different taxa/species were caught visiting this species (Table 4-3). Honeybees were the most frequently observed insects on *O. stricta* flowers, collecting pollen and feeding on nectar throughout the day (08h00 – 13h00) and accumulating large pollen loads ($\bar{x}$ = 134 pollen grains, n = 29) (Table 4-3). *Allodapula* and *Allodape* species were observed collecting mostly pollen in the early morning (10h00) and later evening (from 15h00 onwards) when flowers were closing. *Allodapula* species had the largest pollen loads ($\bar{x}$ = 245 pollen grains, n = 7) while *Allodape* species carried lower pollen loads ($\bar{x}$ = 34 pollen grains, n = 7) (Table 4-3). While these smaller, solitary bees do not visit flowers as frequently as honeybees, they do carry relatively large pollen loads. A single Meliodae visit carried the greatest pollen load (461 pollen grains) but the infrequency of this species suggests it is not an important pollinator of *O. stricta* at this site (Table 4-3). Insects freely move around the open, bowl shaped flowers, coming into contact with both anthers and stigmas and setting off a positive thigmotrophic response, as described above.

4.2.7 Reward preferences in *Opuntia* species

Bees visiting *Opuntia* species seek out different rewards either nectar, pollen or occasionally both. For *O. aurantiaca* 74% of visits were for nectar as a reward (Figure 4-6). The opposite was seen in *O. ficus-indica*, with only 23% of bees collecting nectar and the majority of visits removed pollen as a reward (Figure 4-6). In *O. monacantha* nectar was the preferred reward, being the reward sought in 66% of visits (Figure 4-6). For *O. stricta* reward preference was very similar, with 49% of bees seeking nectar and 51% seeking pollen (Figure 4-6). Bees therefore show significant discrimination between the rewards of three of the four species (χ^2 = 245.2463, df = 3, p < 0.001) (Figure 4-6).

The temporal patterns in pollinator reward choice varied depending on the forage species. The proportion of pollen visits to *O. aurantiaca* remained relatively low and constant throughout the day, while in *O. ficus-indica* the ratio of pollen visits increased through the day (Figure 4-7). Visits to *O. monacantha* were high initially, decreasing around midday, while the number of pollen visits to *O. stricta* continually decreased through the day (Figure 4-7).

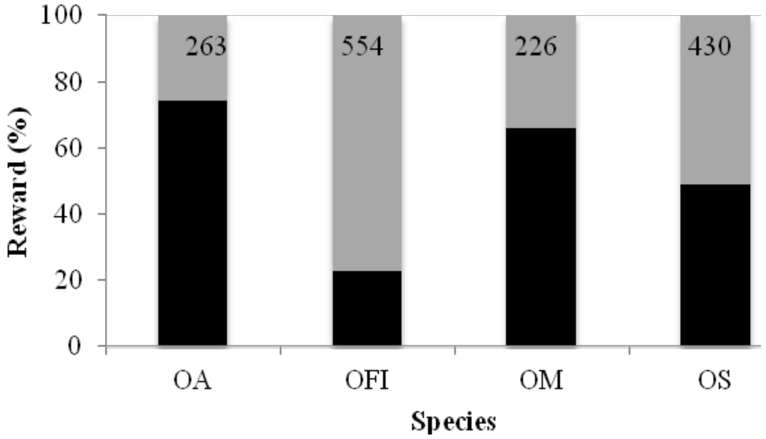


Figure 4-6: Reward preference of all bees visiting flowers of the four species of *Opuntia.* Light grey: pollen reward, dark grey: nectar reward. OA: *Opuntia aurantiaca*, OFI: *Opuntia ficus-indica*, OM: *Opuntia monacantha*, OS: *Opuntia stricta.* Numbers on bars represent sample size. (Pearson's Chi squared test, $\chi^2 = 245.3$, df = 3, $p < 0.001$).

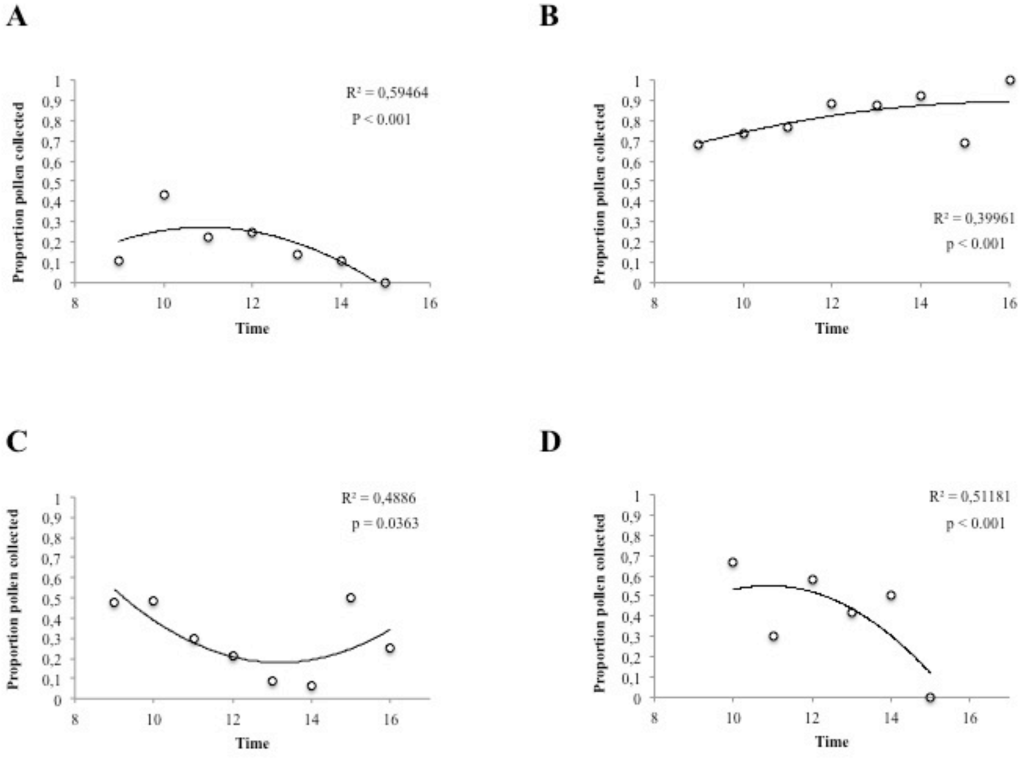


Figure 4-7: Variation in the floral reward preference of bees visiting *Opuntia* species through the day showing the proportion of pollen visits. Observations occurred from 08h00 (denoted by 8) to 16h00 (denoted by 16). A polynomial regression line was fitted. A: *Opuntia aurantiaca*, B: *Opuntia ficus-indica*, C: *Opuntia monacantha*, D: *Opuntia stricta*.

4.2.8 *Pereskia aculeata*

Allodapula species were common visitors to *P. aculeata*, and had moderate pollen loads (x̄ = 106 pollen grains, n = 17) (Table 4-3). Honeybees were also common visitors to this species but none were caught. A single *Allodape* species was caught but had a very low pollen count (28 pollen grains) (Table 4-3). Pollinators were observed between 11h00 and 15h00, after which time flowers would close. Insects' behaviour was similar to the *Opuntia* species with pollinators attracted to the pollen and nectar reward, but to what degree was not quantified.

4.2.9 *Passiflora caerulea*

Xylocopa species were observed with a large quantity of pollen on their thorax and wings making them appear almost yellow (Figure 2-3, E). Their size means they come into direct contact with the anthers and stigmas when feeding on nectar suggesting they are efficient pollinators of *P. caerulea* (Appendix 1: Supplementary Video 3, A - E). This was not directly reflected in the number of pollen grains (from 7 - 32) counted on *Xylocopa* species (Table 4-3), possibly due to loss occurring when caught in the net, or the number of visits recorded. *X. falvicollis* was observed to visit 1 flower before flying off, while *Xylocopa flavorufa* (DeGeer) visited several flowers in a population at one time. Observations showed that carpenter bees come into direct contact with the stigmas on entering and exiting after feeding on nectar. The infrequency of carpenter bee visit suggests they may not be common pollinators but there efficiency should not be discredited. Visits mostly occurred around midday and throughout the afternoon.

Honeybees more commonly visited *P. caerulea* flowers, with up to 7 honeybees observed feeding on nectar from one flower, though usually only 1 - 3 honeybees were on a flower at any given time. Honeybees had the greatest pollen loads ($\bar{x}$ = 106 pollen grains, n = 14) (Table 4-3) and were observed to land on or walk over anthers before and after feeding on nectar. This could account for there relatively large pollen count. Visits to flowers occurred from flower opening until late afternoon.

Birds have been observed visiting the flowers around Grahamstown, probably feeding on nectar but this was mostly observed from a distance. A bird was observed defending the flowers from an *X. flavorufa* bee visiting the plant. A female sunbird was observation visiting flowers near Kingswood School, Grahamstown by Dr Craig Peter, a bird was observed removing nectar from *P. caerulea* flowers on Rhodes University campus, and Figure 2-3 (F) shows a bird removing nectar from a flower of *P. caerulea*, near Shepperson Avenue, Grahamstown .

4.2.10 *Solanum chrysotrichum*

A variety of *Xylocopa* species were observed visiting flowers and on two occasions a high ferquency vibration was heard indicating buzz pollination. Unfortunately no *Xylocopa* species were caught. Two *Allodapula* species were caught but had very low pollen counts ($\bar{x}$ = 2 pollen grains) suggesting little or no contribution to pollination (Table 4-3).

4.2.11 *Solanum mauritianum*

A total of six different taxa were caught visiting this species (Table 4-3). Honeybees were the most common visitors (Table 4-3), being observed throughout the day. *S. mauritianum* has poricidal anthers indicative of buzz polliantion yet honeybees are thought to be unable to sonicate the anthers. I did however observe honeybees manipulating the poricidal anthers to remove pollen by flicking the anthers with their heads and pollen counts suggest they are abe to effectively remove pollen ($\bar{x}$ = 1729 pollen grains, n = 16) (Appendix 1: Supplementary Video 4; Table 4-3). Eleven *Xylocopa* species were caught visiting flowers of *S. mauritianum* and all had relatively large pollen laods, varying from $\bar{x}$ = 61 pollen grains (n = 3) for *X. falvicollis* to $\bar{x}$ = 7525 pollen grains (n = 4) for *X. flavorufa*, with one insect carrying 14 919 pollen grains (Table 4-3). *Allodpaula* species had the greatest pollen count ($\bar{x}$ = 9472 pollen grains, n = 3) (Table 4-3). These high pollen loads suggest that these insects contribute to the successful pollination of this species.

4.2.12 Inferring visitation rates by the presence of pollen in poriocidal anthers in *Solanum* species

The number of anthers containing pollen was scored to estimate visitation rates to flower. Only 5% of *S. chrysotrichum* anthers had all their pollen removed from a single flower, 12% had pollen removed from all but one anther on a flower and the remaining 84% still had two or more anthers with pollen (Figure 4-8). Similarily, *S. mauritianum* had 7% of all anthers from a single flower lacking pollen, 13% had pollen removed from all but one anther on a flower while 80% still had two or more anthers on a flower with pollen present (Figure 4-8).

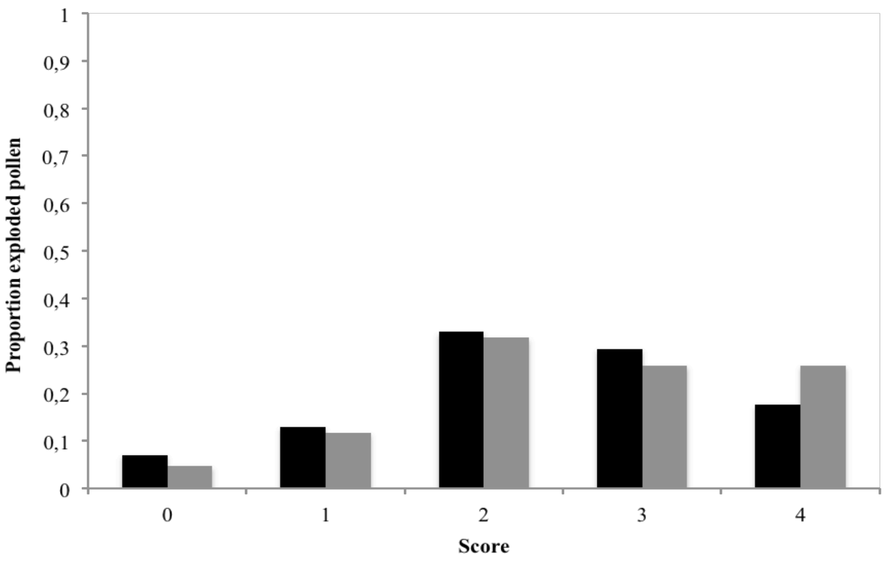


Figure 4-8: Pollen ejected from anthers in response to artificial sonication. Black: *Solanum mauritianum* and Grey: *Solanum chrysotrichum*. A score of 0 means no pollen ejected from the 4 anthers tested, 1 indicates pollen exploded from 1 out of 4 anthers, 2 means 2 out of 4 anthers, 3 means 3 out of 4 anthers respectively, and 4 means pollen exploded from all anthers tested.

4.2.13 *Yucca aloifolia*

Y. aloifolia flowers remained open throughout the day and night. Honeybees were the only insects caught and observed visiting this species despite night observations. Three evening observations (from sunset to 21h30) showed no evidence of moths visiting flowers.

Honeybees had relatively high average pollen loads ranging from 2 pollen grains to 2578 pollen grains (x̄ = 739 pollen grains, n = 15) (Table 4-3). Honeybees were caught on plants in both Port Alfred and Grahamstown. Observations of the honeybees showed activity continued throughout the day, with one bee even being observed after sunset. The behaviour of the honeybees varied with some removing nectar from the external parts of flowers, possibly from extrafloral nectaries, while other would enter a flower, removing pollen from the stigmatic base. Due to the morphology of the flower, honeybees would come into contact with the anthers upon entering the flower. This suggests that honeybees are feeding on the nectar of *Y. aloifolia* and contributing to their pollination.

The volume and concentration of nectar was recorded over a 10 hr period for both bagged and unbagged flowers. The volume and concentration for bagged and unbagged flowers both showed a similar trend (Figure 4-9). Unbagged flowers had a consistently lower volume and concentration of nectar throughout the day compared with bagged flowers, with nectar volume dropping from 8.1 µl at 08h00 to 0.2 µl by 18h00, and concentration falling from 12% to 2% (Figure 4-9). Bagged flowers had a volume of 28 µl at 08h00, 25 µl at 12h00 (compared with unbagged volume of 3.7 µl) which dropped to 3 u µl at 18h00 (Figure 4-9). The concentration of nectar in bagged flowers remained above 10% (18% at 08h00, 26% at 12h00 and 11% at 18h00), compared with unbagged flowers where the concentration had dropped below 5% by 12h00 (Figure 4-9).

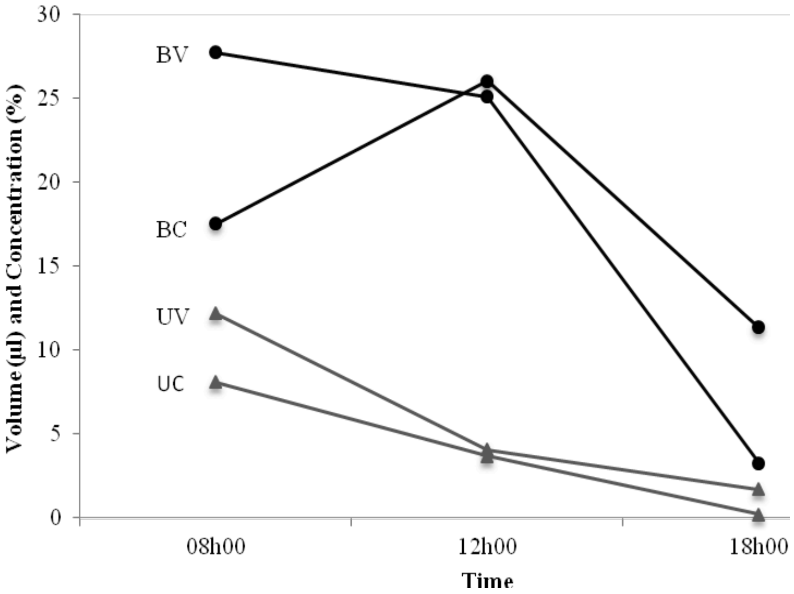


Figure 4-9: Changes in nectar volume and concentration for bagged and unbagged *Yucca aloifolia* flowers, from dawn to dusk. BV: Bagged volume, BC: bagged concentration, UV: unbagged volume and UC: unbagged concentration. N equals 10 for each treatment.

Table 4-3: Pollinators and their pollen loads recorded for 11 alien plant species.

Plant species	**Pollinator**	**N**	**No. of pollen grains** (x̄ ± SD)
Acacia longifolia	*Apis mellifera* (Apidae)	21	77 ± 160
	Allodape species (Apidae)	1	23
	Allodapula species (Apidae)	1	3
	Asarkina africana (Syrphidae)	2	3 ± 1
Melia azedarach	*Apis mellifera* (Apidae)	16	664 ± 769
	Polistes africanus (Apidae)	2	33 ± 45
	Xylocopa caffra (Apidae)	1	2716
	Xylocopa flavicollis (Apidae)	11	976 ± 949
	Chrysomelidae	1	6
	Cucujoidea	1	11
	Diptera	1	2
	Nitidulidae (cf)	1	4
	Crytothyrea marginalis (Scarabaeidae)	1	33 ± 45
	Tachinidae	2	236 ± 270
Opuntia aurantiaca	*Apis mellifera* (Apidae)	24	212 ± 177
	Anthophora (Heliophila) wartmanni (Apidae)	1	24
Opuntia ficus-indica	*Apis mellifera* (Apidae)	28	141 ± 125
Opuntia monacantha	*Apis mellifera* (Apidae)	3	233 ± 72
	Allodape species (Apidae)	1	179
Opuntia stricta	*Apis mellifera* (Apidae)	29	134 ± 115
	Allodape species (Apidae)	7	34 ± 66
	Allodapula species (Apidae)	7	245 ± 35

Plant species	**Pollinator**	**N**	**No. of pollen grains** (x̄ ± SD)
Opuntia stricta (cont.)	*Nomia* species (Halictidae)	1	4
	Meloidae	1	461
Pereskia aculeata	*Allodape* species (Apidae)	1	28
	Allodapula species (Apidae)	17	280 ± 170
Passiflora caerulea	*Apis mellifera* (Apidae)	14	106 ± 234
	Allodape species (Apidae)	1	6
	Xylocopa caffra (Apidae)	1	21
	Xylocopa flavicollis (Apidae)	2	7 ± 7
	Xylocopa flavorufa (Apidae)	1	32
Solanum chrysotrichum	*Allodapula* species (Apidae)	2	2 ± 1
	Melyrides (cf)	1	1
Solanum mauritianum	*Apis mellifera* (Apidae)	16	1 729 ± 2 774
	Allodapula species (Apidae)	3	9 472 ± 12 218
	Xylocopa caffra (Apidae)	4	2 920 ± 3 469
	Xylocopa flavicollis (Apidae)	3	61 ± 33
	Xylocopa flavorufa (Apidae)	4	7 525 ± 6 823
	Dejeania bombylans (Tachinidae)	1	10
Yucca aloifolia	*Apis mellifera* (Apidae)	15	739 ± 845

4.3 Pollen limitation and Indices

4.3.1 *Acacia longifolia*

Fruit set for pollen supplementation and control was significantly different ($F_{(2,67)} = 3.66$, $p = 0.03$), with pollen supplementation being different to the control (Figure 4-10, A). There was no significant difference in the average number of seeds per fruit ($F_{(1,30)} = 2.2$, $p = 0.152$) between the three treatments (Figure 4-10, A). The PLI at the level of fruit set supports this species not being pollen limited (Table 4-4).

4.3.2 *Melia azedarach*

Fruit set in *M. azedarach* showed no significant difference ($F_{(1,33)} = 0.77$, $p = 0.084$) (Figure 4-10, B). There was also no significant difference between mean fruit weight ($F_{(1,33)} = 1.3$, $p = 0.269$) but there was a significant difference in the average number of seeds per fruit ($F_{(1,33)} = 5.7$, $p = 0.023$) (Figure 4-10, B). This is supported by the PLI at the level of fruit and seed set, suggesting no pollen limitation (Table 4-4).

4.3.4 *Opuntia aurantiaca*

Fruit set was 71% for pollen supplementation while the control had 100% fruit set but there was no significant difference between the two treatments ($F_{(1,26)} = 2.21$, $p = 0.149$) (Figure 4-10, C). There was also no significant difference between mean fruit weight ($F_{(1,33)} = 2.3$, $p = 0.140$) and average number of seeds per fruit suggesting this species is not pollen limited ($F_{(1,33)} = 1.8$, $p = 0.195$) (Figure 4-10, C). The average seed weight for pollen supplementation was 0.04 g for pollen supplementation and 0.02 g for control but all the seeds were brown and immature (Figure 4-10, C). Lack of pollen limitation is further supported by the low PLI at the level of fruit set (Table 4-4).

4.3.4 *Opuntia ficus-indica*

The PLI at the level of fruit and seed set indicates this species is not pollen limited (Table 4-4) and this is supported by the 100% fruit set in both pollen supplementation and control treatments (Figure 4-10, D). There was no significant difference between fruit set ($F_{(1,55)} = 0.006$, $p = 0.941$), mean fruit weight ($F_{(1,55)} = 1.1$, $p = 0.3$) and the average number of mature seeds per fruit ($F_{(1,55)} = 0.4$, $p = 0.535$) (Figure 4-10, D).

Pollen supplementation produced 305 seeds on average and control produced 286 seeds (Figure 4-10, D), and only 39% of control seeds matured, while 53% of seeds in the pollen supplementation treatment matured (i.e. were whole black seeds). This suggests this species does not suffer from pollen limitation in the invasive range.

4.3.5 *Opuntia monacantha*

High levels of fruit set where observed in *O. monacantha*, but no significant difference was observed,($F_{(1,43)} = 1.18$, $p = 0.284$) (Figure 4-10, E). There was also no significant difference in mean fruit weight ($F_{(1,38)} = 2.0$, $p = 0.168$) and the average number of mature seeds per fruit ($F_{(1,38)} = 2.1$, $p = 0.157$) (Figure 4-10, E) suggesting this species does not suffer from pollen limitation. Pollen supplementation produced 65 seeds while control only produced 51 seeds (Figure 4-10, E), but only 2% of pollen supplementation seeds developed into possibly viable seeds versus 0% for the control. The PLI at the level of fruit set shows low levels of pollen limitation, while at the level of seed set, medium levels of pollen limitation were observed, suggesting this speices may be partially pollen limited (Table 4-4).

4.3.6 *Opuntia stricta*

Supplementation of pollen on stigmas had no significant effect on the percentage fruit set between pollen supplementation and control ($F_{(1,49)} = 0.39$, $p = 0.538$) (Figure 4-11, F). There was also no significant difference in mean fruit weight ($F_{(1,46)} = 0.5$, $p = 0.473$) and the average number of mature seeds per fruit ($F_{(1,46)} = 0.1$, $p = 0.761$) (Figure 4-11, F). According to the PLI at the fruit and seed level this species is not pollen limitated (Table 4-4).

4.3.7 *Passiflora caerulea*

No pollen limitation was evident in the fruit set ($F_{(1,92)} = 2.08$, $p = 0.152$), mean fruit weight ($F_{(1,10)} = 0.9$, $p = 0.372$) and mean number of seeds per fruit ($F_{(1,10)} = 0.7$, $p = 0.412$) for *P. caerulea* (Figure 4-11, G). Pollen supplementation treatment set 22% fruit (77% matured) while the control set 16% fruit (89% matured) (Figure 4-11, G). A high level of pollen limitation is suggested for this species by the high PLI value of 0.43 (Table 4-4). Pollen limitation was not evident from the pollen supplementation experiment, though the PLI value at the level of fruit set was high, therefore indicating *P. caerulea* might be pollen limited.

4.3.8 *Pereskia aculeata*

There was no significant difference in the fruit set of *P. aculeata* ($F_{(1,52)} = 0.77$, $p = 0.999$). Fruit set was 0% for pollen supplementation and 1% for the control treatment and no seeds were observed in the single fruit.

4.3.9 *Solanum chrysotrichum*

No significant difference was observed in the fruit set of *S. chrysotrichum* ($F_{(1,50)} = 0.10$, $p = 0.755$) (Figure 4-11, H). There was also no significant difference in mean fruit weight ($F_{(1,37)} = 0.00$, $p = 0.978$) and average number of seeds per fruit between the pollen supplementation treatment and control ($F_{(1,37)} = 1.1$, $p = 0.294$) (Figure 4-11, H). This species is not pollen limited at the level of fruit and seed set (Table 4-4).

4.3.10 *Solanum mauritianum*

There was no significant difference in the percentage fruit set for pollen supplementation and control ($F_{(1,32)} = 0.02$, $p = 0.999$) (Figure 4-11, I). There was also no significant difference in the mean fruit weight ($F_{(1,26)} = 0.08$, $p = 0.782$) and the average number of seeds per fruit ($F_{(1,26)} = 0.04$, $p = 0.849$) (Figure 4-11, I). This species is not pollen limited at the level of fruit and seed set (Table 4-4).

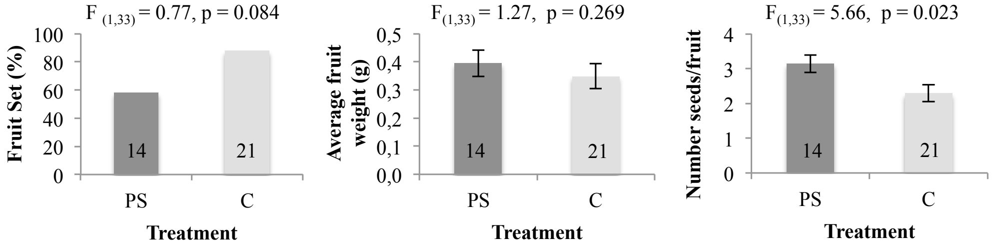
4.3.11 *Yucca aloifolia*

No significant difference was observed in the percentage fruit set ($F_{(1,70)} = 0.71$, $p = 0.401$) and mean fruit weight between pollen supplementation and control ($F_{(1,11)} = 0.1$, $p = 0.761$) (Figure 4-11, J), yet the high PLI value at the level of fruit and seed set for this species suggests pollen limitation (Table 4-4). There was also no significant difference in the average number of mature seeds between pollen supplementation and control ($F_{(1,11)} = 0.9$, $p = 0.377$) (Figure 4-11, J). More pollen supplementation seeds matured (20%), while only 6% of control seeds matured.

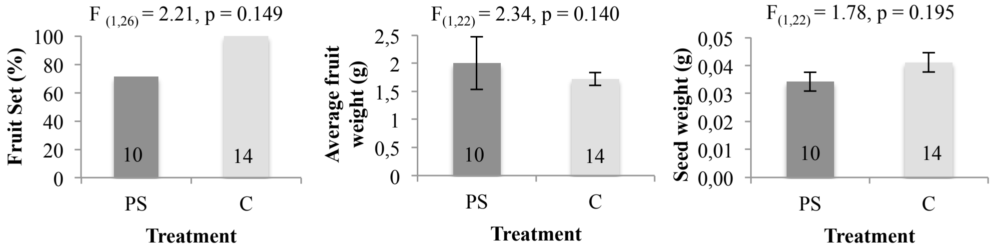
Pollen limitation was not evident from the pollen supplementation experiment, though the PLI value was high, therefore indicating *Y. aloifolia* might be pollen limited.

A. *Acacia longifolia*

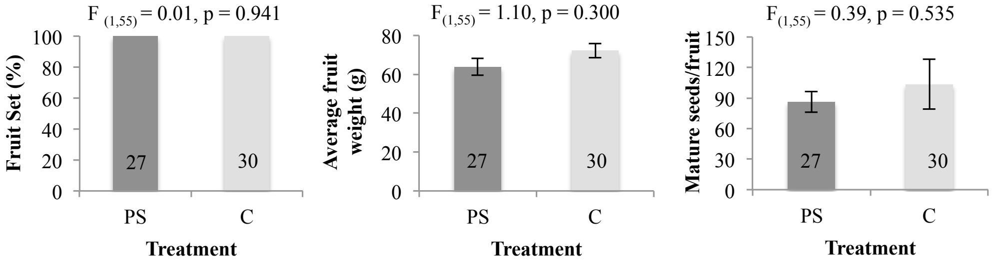
B. *Melia azedarach*



C. *Opuntia aurantiaca*



D. *Opuntia ficus-indica*



E. *Opuntia monacantha*

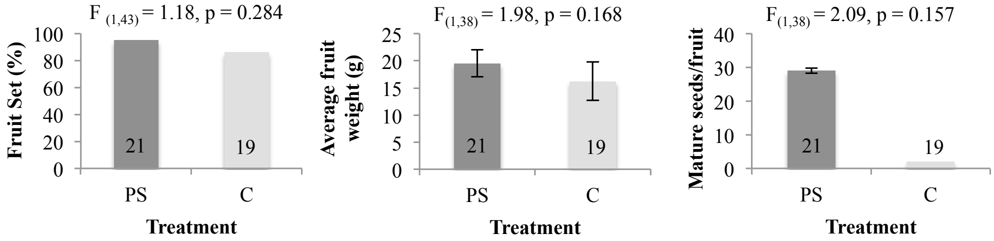
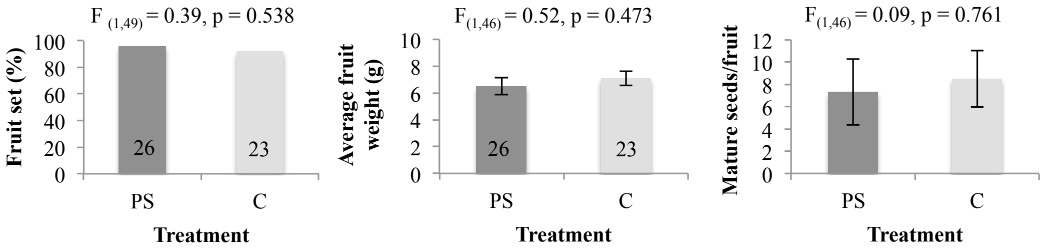
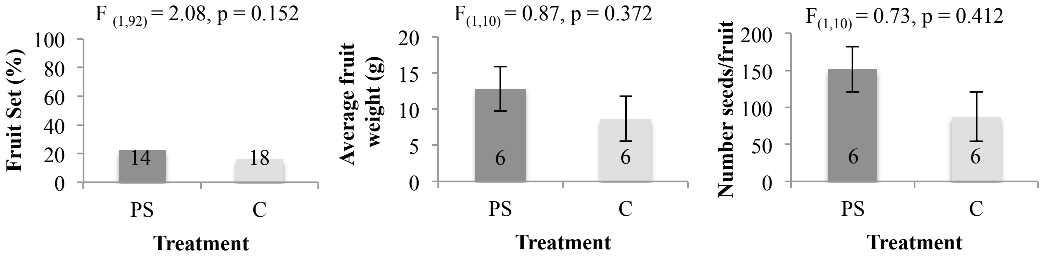


Figure 4-10: Effect of pollen supplementation on fruit set, fruit weight and number of seeds for 5 invasive species. PS: Pollen supplementation, A: autonomous self-pollination and C: open control. Standard error bars are displayed. Numbers associated with bars represent sample size.

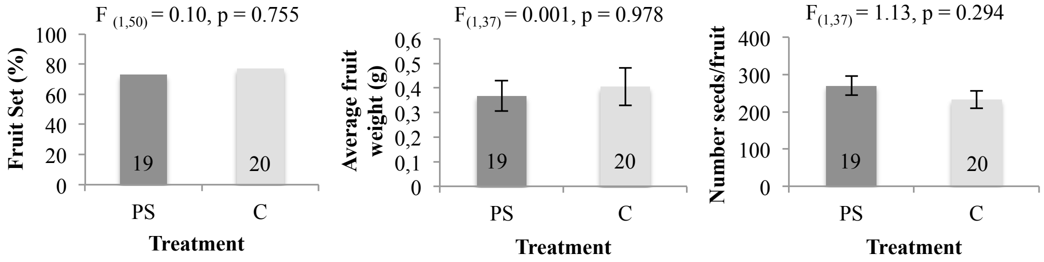
F. *Opuntia stricta*



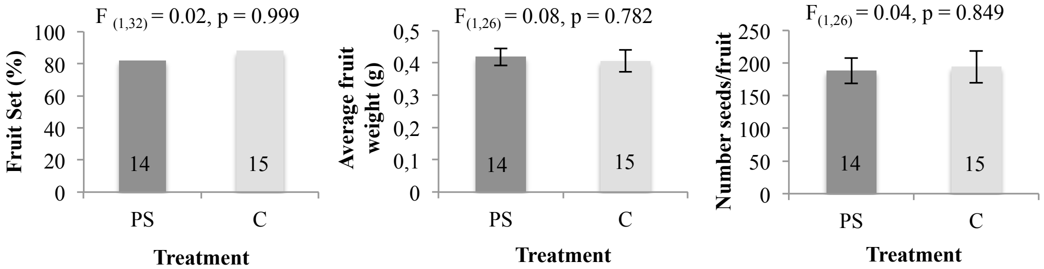
G. *Passiflora caerulea*



H. *Solanum chrysotrichum*



I. *Solanum mauritianum*



J. *Yucca aloifolia*

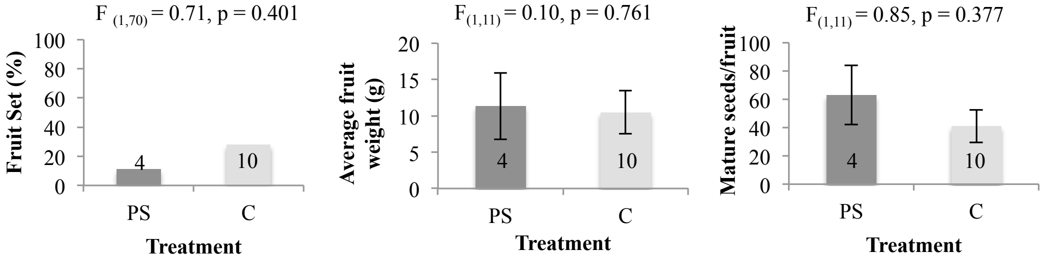


Figure 4-11: Effect of pollen supplementation on fruit set, fruit weight and number of seeds for 5 invasive species. PS: Pollen supplementation and C: open control. Standard error bars are displayed. Numbers associated with bars represent sample size.

Table 4-4: Using indices to assign a pollen limitation rating to 11 invasive species at the level of fruit set and to assign a pollen limitation rating to 8 species at the level of seed set. PLI: Pollen Limitation Index, PLI ≤ 0 suggests *no* pollen limitation, PLI < 0.25 indicates *low* levels of pollen limitation, 0.25 < PLI < 0.75 indicates *medium* levels of pollen limitation and PLI > 0.75 indicates *high* levels of pollen limitation, PL: pollen limitation. Dash (-) indicates lack of data available for the species.

Plant Species	**PLI (fruit set)**		**PLI (seed set)**	
	Value	**Value**	**Value**	**Value**
A. longifolia	0.00	No PL	-	-
M. azedarach	- 0.50	No PL	-0.01	No PL
O. aurantica	- 0.40	No PL	-	-
O. ficus-indica	0.00	No PL	0.06	No PL
O. monacantha	0.10	Low PL	0.30	Medium PL
O. stricta	0.04	Low PL	0.15	No PL
P. caerulea	0.43	High PL	-	-
P. aculeata	-	-	-	-
S.chrysotrichum	- 0.05	No PL	0.09	No PL
S. mauritianum	- 0.07	No PL	-0.03	No PL
Y. aloifolia	0.50	High PL	0.63	High PL

4.4 Growth trials, seed germination and asexual root production by fruit

4.4.1 Growth trial of *Opuntia aurantiaca* seeds

O. aurantiaca in South Africa is believed to be a sterile clone therefore we planted all the brown seeds produced from the breeding system experiment in a greenhouse. Results showed that after 3 years no seedlings had emerged, supporting the idea of this species being a sterile clone.

4.4.2 Growth trial and dispersal mechanism in *Opuntia ficus-indica*

A greenhouse experiment involving fertile black and infertile brown seeds of *O. ficus-indica* produced no seedlings in the first year (2012). During the second year (2013) 25% or 8 seedlings emerged and all except one were from fertile black seeds. The 'brown' infertile seed that developed may have resulted from a black fertile seed accidentally mixing with infertile brown seeds. In the third year (2014) seedling emergence was still 25% and seedlings had grown in size, with one seedling now consisting of 4 cladodes and measuring over 30 cm in height.

4.4.3 Fruit rooting and dispersal in *Opuntia* species

Upon harvesting of fruit, rooting was observed in some *Opuntia* species suggesting the whole fruit may function as asexual propagules. No rooting was observed on *O. aurantiaca*, 18% of harvested *O. ficus-indica* fruit developed roots, 57% of harvested *O. monacantha* fruits developed roots and 68% of harvested *O. stricta* fruits rooted suggesting these species are capable of reproducing both sexually and asexually from fruit (Figure 4-12, A - C). Furthermore, fruit of *Opuntia* species has been observed in rivers and washed up on beaches in the Eastern Cape, sometimes with roots and well developed cladodes, suggesting rivers and ocean currents can play a role in their dispersal in South Africa. Figure 4-12 (D) shows *Opuntia* fruit washed up on a beach near the Great Fish River after heavy rain.

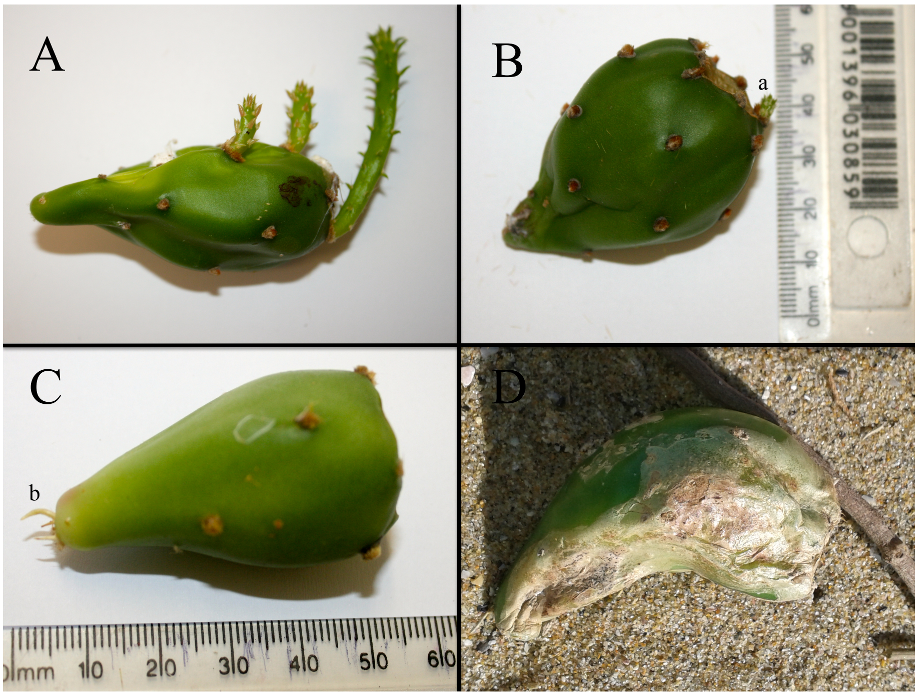


Figure 4-12: Rooting in *Opuntia* species and evidence of fruit washed ashore. A: *Opuntia monacantha* with three cladodes protruding from the fruit, B: *Opuntia monacantha* starting to produce a cladode (a), C: *Opuntia stricta* with small roots (b), D: *Opuntia* species washed ashore near Fish River Mouth.

4.4.4 Growth trial for *Yucca aloifolia*

For the greenhouse experiment black (viable) seeds planted in rows yielded 100% seedling emergence. There was also 100% seedling emergence with seedlings scattered on the surface of the soil.

The field experiment consisted of two treatments, planting black fertile seeds and leaving half fruits on the surface (Figure 4-13, A - C). The rate of germination for from half fruits was 0 at interval one (March 2014) and remained constant at 0.008 for interval 2 (August 2014) and interval 3 (October 2014) (Table 4-5). The germination rate for seedlings from half a fruit buried below the surface decreased over time, starting at 0.259 in March 2014, decreasing to 0.229 in August 2014 and 0.204 in October 2014 (Table 4-5). The average number of seedlings that emerged from half a fruit was 0 (Figure 4-13, B) for all three dates while the number of seedlings from planted seeds was 13, 11 and 10 respectively for the three sampling dates (Figure 4-13, B and D). The number of seedlings from seeds decreased over the year period with evidence of browsing and seedling death observed during the final count. This suggests that new *Y. aloifolia* plants may established from seeds under natural conditions and therefore spread may not just be via clonal growth.

Table 4-5: Germination rate, or the number of seedlings that emerged divided by the average number of seeds per fruit, for *Y. aloifolia* from a field experiment in Port Alfred

Observation Interval	Germination rate	
	Half Fruit	Seed
March 2014	0.000	0.259
August 2014	0.008	0.229
October 2014	0.008	0.204

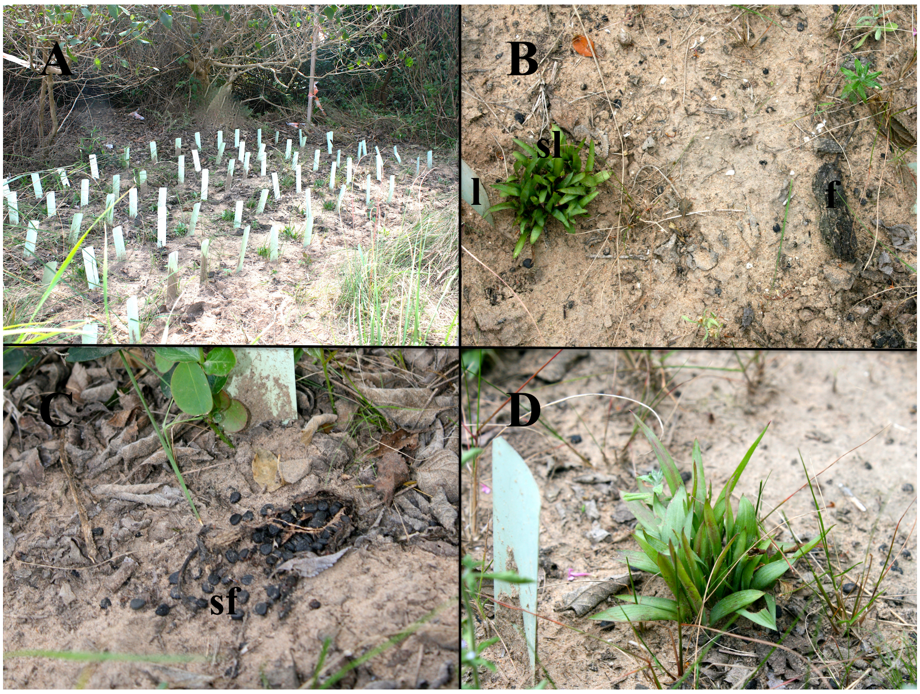


Figure 4-13: *Yucca aloifolia* field germination trial. A: Field site on Standerwick Farm, Port Alfred, B: bet up of trial showing label (l), a clump of seedlings (sl) growing from planted seeds and a fruit (f) lying on the surface, C: black fertile seeds (sf) were used in the field germination trial, D: *Yucca aloifolia* seedlings growing from seed planted in the soil.

Chapter 5: Discussion

5.1 Baker's Law and the breeding system of invasive plants

I tested the hypothesis that all study species would be self-compatible and capable of uniparental reproduction, with my results providing evidence to support this. Of the eleven invasive species investigated, eight species are self-compatible, ten species are capable of autonomous self-pollination, and three species showed evidence of self-incompatibility. The high levels of fruit and seed set among ten of the invasive species investigated may be a result of autonomous self-pollination. *P. aculeata* was also able to reproduce vegetatively, allowing for uniparental reproduction and therefore colonization. This strongly supports Baker's Law that an individual capable of uniparental reproduction is more likely to produce offspring than two self-incompatible individuals after long-distance dispersal, and that autonomous self-pollination allows for successful colonization (Baker, 1955, 1965). All except one species (*P. caerulea*) are self-compatible to varying degrees, but *M. azedarach*, *A. longifolia* and *P. aculeata* all exhibiting very low levels of self-compatibility. Nevertheless, some seed set was recorded in the self-pollination and autonomous self-pollination treatments for these species. The *Opuntia* and *Solanum* species all exhibited high levels of self-compatibility, setting abundant fruit in the self-pollination and autonomous self-pollination treatments. All other species had similar or higher rates of cross-pollination compared to self-pollination. Fruit production via autonomous self-pollination and cross-pollination is high, and the seed production by these invasive species (except *P. aculeata*) is likely allowing new individuals to establish. This supports that idea that the establishment and success of these invasive species could be due to their reproductive strategies, with similar findings in South Africa by Rambuda and Johnson (2004) who found all 17 invasive plant species studied in South Africa to be self-compatible or apomictic, and 72% capable of autonomous self-pollination, Moodley *et al* (2015) who found five *Banksia* species and *H. salicifolia* to be capable of autonomous self-pollination and a study on Iridaceae from South Africa which have become invasive around the world showed them to be capable of autonomous self-pollination compared with species that had not become naturalized (van Kleunen *et al*, 2008). Invasive plant species in South Africa show a trend towards the ability to undergo autonomous self-pollinate or reproduce vegetatively, thereby enabling colonization.

Baker's law was initially conceived to explain colonization on oceanic islands after long distance dispersal (Baker, 1955, 1965), but has since been used to explain processess, such as species invasion, more broadly (Pannell, 2015). If colonization involved a single, or few individuals one would expect self-compatibility or the ability to self-fertilize be common (Pannell, 2015). Studies however provide evidence both supporting and contradicting this theory. Evidence supporting Baker's law has been accumulated from around the world. In China, Hao *et al* (2011) compared 12 invasive Asteraceae with a global database of Asteraceae and found 67% to be self-compatible and 83% set seed via autonomous self-pollination compared to the 36,8% and 46% respectively in the global database. Yan *et al* (2015) found *Bidens frondosa* (L.) (Asteraceae) to be a successful invader as it utilized both self- and cross-pollination, easily adapting to either reproductive strategy. Of 361 species that arrived in the USA from Europe, a significant number were capable of either autonomous self-pollination or were self-compatible, and these species had a larger invasive range compared with self-incompatible species. Furthermore, those that depended on pollinators had a significantly smaller invasive range compared with species that were independent of pollinators (van Kleunen and Johnson, 2007a). Self compatibility has been been found in a number of species including garlic mustard (*Alliaria petiolata*) in North America (Cavers et al. 1979), the Hottentot fig (*Carpobrotus edulis*) in California (Vilà et al. 1998) and *Carpobrotus affine acinaciformis* and *O. stricta* in Spain (Bartomeus and Vila, 2009), with these species providing evidence in support of Baker's Law, and the invasive *Kalanchoe daigremontiana* (or *Bryophyllum daigremontianum*) in Venezuela, is autogamous and relies on clonal growth for its spread (Herrera and Nassar, 2009). Some invasive species, like three invasive milkweeds in Australia (*A. curassavica*, *G. fruticosus* and *G. physocarpus*) rely on pollinators for seed set but are self-compatible, even though the majority of milkweeds are known to be self-incompatible (Coombs *et al*, 2009; Ward *et al*, 2012). *Stepilia gigantea* (N. E. Br) (Asclepiadoideae), originally from South Africa is a self-incompatible species now invasive in Venezuela, where local carrion flies are responsible for abundant seed set (Herrera and Nassar, 2009). Most of the species investiagted in this study where self-compatible in both their native and invasive range, and some species, especially the Cactaceae are capable of vegetative reproduction, i.e. they are capable of uniparental reproduction, supporting Baker's Law.

As noted above, not all invasive plant species need to be self-compatible in order to successfully colonize a new habitat. Self-incompatible species can also successfully invade a new area if they arrive in sufficient numbers and can co-opt pollinators. Of the species investigated in this study, three species where self-incompatible in their native range, namely *A. longifolia*, *P. caerulea*, *P. aculeata*, though all three species showed the ability for self-compatibility in South Africa. Some invasive species are self-incompatible in both their native and invasive range.. *Paederia foetida* (L.) (skunk vine) in Florida, USA, is self-incompatible, relying on native and introduced pollinators for seed set (Liu *et al*, 2006), *Araujia sericifera* is South Africa is not capable of autonomous self-pollination, making this species entirely reliant on bees for pollination and fruit set (Coombs and Peter, 2010) and *Stapelia gigantea* in Venezuela is self-incompatible, relying on native pollinators for seed set (Herrera and Nassar, 2009). Other factors could also contribute to the colonization and invasive success of a species, with Lafuma and Maurice (2007) suggesting the self-incompatible herb *Senecio inaequidens* was able to colonize due to ecological factors, such as being a generalist and having immense seed set, not because of the breeding system. Additionally, it has been found that the degree of self-compatibility and self-incompatibility can vary, with Petanidou *et al* (2012) finding the variation between self-compatibility and self-incompatibility in species varied within the native and invasive range, as well as between populations of species in their native and invasive ranges. Self-incompatibility does not prevent a species from becoming invasive, but it is thought that self-compatible species are more likely to become successful colonizers. It has also been found that even species which are highly self compatible, and set fruit via autonomous self-pollination, can rely on pollinators in their invasive range to increase seed set and thus aid in the invasion process (Rodger *et al*, 2010).

5.2 Importance of pollinators in facilitating invasions

I tested the hypothesis that all study species have co-opted native pollinators and that they are contributing to successful seed set. When encountering a new environment it is often crucial for invasive plants (especially self-incompatible species) to find suitable mates, of the same species, with viable pollen, and/or pollinators to facilitate the movement of pollen from anther to stigma (Harmon-Threatt *et al*, 2009; Richardson, *et al*, 2000b). Finding suitable pollinators can be achieved by either (a) bringing mutualistic pollinators from the native range (b) co-opting resident pollinators in the new range (c) waiting for a specialist pollinator to be introduced (Bjerknes *et al*, 2007; Harmon-Threatt *et al*, 2009; Parker and Haubensak, 2002; Richardson *et al*, 2000b) or (d) waiting until selection produces traits in the plant that are suitable to the available pollinators. *Lilium formosanum* Wallace (Liliaceae) is native to Taiwan but has become invasive in South Africa, where it has a specialized pollination system and is capable of autonomous self-pollination (Rodger *et al*, 2010). In South Africa it has co-opted a local pollinator, a long tongued hawk moth *Agrius convlvuli* (Linnaeus), which resulted in increased seed set in both cross-pollination and open treatments, suggesting a specialized pollination system and self-compatibility are not limiting factors to an invasive species spread (Rodger *et al*, 2010). Outcrossing by co-opted local pollinators is thus increasing genetic variability within population of *L. formisanum* (Rodger *et al*, 2010). Co-opting suitable local pollinators may be problematic for invasive plants, especially those with highly specialized pollination systems.

The species investigated however, appear to be independent of pollinators, mostly setting seed in the absence of pollinators, though cross-pollination by local pollinators possibly allows for some degree of genetic variation within populations. Despite this, all eleven invasive plant species are regularly visited by a variety of generalist pollinators including honeybees, carpenter bees and *Allodapini* species. Pollinators all carried substantial pollen loads, even managing to extract pollen from more specialized plants, and frequently came into contact with both anthers and stigmas. Considering most of theses species are capable of autonomous self-pollination, their reliance on pollinators may be low, with pollinators possibly only serving to facilitate outcrossing to some degree. Baker’s Law proposed that invasive plant species with a generalised pollination system would be more successful invaders compared to specialized species, as they can easily co-opt local pollinators from the broad range that is available (Baker, 1955, 1965; Johnson and Steiner, 2000; Rambuda and Johnson, 2004), and further predicted that invasive species need not rely heavily on pollinators as their breeding systems usually enables reproduction in the absence of a mate and/or pollinators, but evidence is mounting that suggests even self-compatible species still rely on pollinators for reproduction (Liu *et al*, 2006; Hong *et al*, 2007; van Kleunen and Johnson, 2005; Ward and Johnson, 2013). From the breeding system results above, we know that most of the species from this study are capable of autonomous self-pollination, thus negating the need for both pollinators and a mate. Pollinators are therefore probably contributing little to the reproductive success of these invasive plant species.

Flowering in these invasive species varied throughout the year, with *S. chrysotrichum* and *S. mauritianum* flowering throughout the year. Other species such as *A. longifolia* and *P. aculeata* only flower during the winter months, thus providing pollinators with a pollen source during the colder months when fewer native species are flowering. Other more seasonal species such *O. ficus-indica* and *O. stricta* flower during the summer months when more native species are flowering yet do not appear to suffer any pollen limitation as a result.

5.2.1 Pollinators in native and introduced range

Honeybees were the dominant visitors to *A. longifolia*, with other species being less common visitors in the Eastern Cape, South Africa, and in its native range, non-native honeybeesare the main pollinator of *A. longifolia*, with other species being found in lower abundance (Bernhardt, 1987). In South Africa, Australian *Acacias* are known to be visited by native honeybees (*Apis mellifera*), but also flies and bees (Gibson *et al*, 2011). This species flowers in the winter months in South Africa, providing a source of pollen for insects during this period. There are no studies documenting pollinators of *M. azedarach*, but it was suggested that the fragrant flowers are insect pollinated, possibly by moths and bees (Waggy, 2009). No pollinators were observed visiting flowers in 2012, supporting the findings of Rambuda (2001). This could be attributed to local weather conditions (strong winds and rain) during the flowering period. However, in 2013 a wide variety of pollinators were caught and observed heavily utilizing the flowers during the flowering period. Despite the small flower, low levels of nectar and relatively narrow tube this species appears to be a generalist in the invasive range.

Small to large hymenopterans appear to be the pollinators of *Opuntia* species, with size of the visiting insect depending on the flower size (Reyes-Aguëro *et al*, 2006). In South Africa, *A. mellifera* was found to be the main pollinator of *O. aurantiaca* (even though it is listed as infertile and of hybrid origin, so reliance on pollinators is probably negligible (Archibald, 1936), *O. ficus-indica* and *O. monacantha*. Beinart and Wotshela (2012) suggested that Cape bees and some local bird species visit flowers of *O. ficus-inidca* in South Africa and in Italy 50 different species were caught visiting flowers (Lo Verde and La Mantia, 2011), but results suggested only a few of the visiting insect species are effective pollinators (Lo Verde and La Mantia, 2011). In the native range, Brazil, a variety of species including bees, ants and beetles were recorded visiting *O. monacantha* flowers, with bees coming into direct contact with the stimgas, mostly collecting pollen as a reward (Lenzi and Orth, 2011, 2012). Along the French Mediterranean, where *O. monacantha* is naturalized, six bee species reguarly visit flowers, including *A. mellifera* and *X. violacea* (Linnaeus) (Daumann, 1930 in Grant and Hurd, 1979) with *Xylocopa* species observed visiting *O. monacantha* in the Eastern Cape. *O. stricta* was also visited by a number of insects including honeybees and *Allodapini* species in the invasive range of the Eastern Cape. In its native range, Florida, USA, Spears Jr. (1987) found eight different insect visitors on *O. stricta*, with three species being regular visitors - *A. mellifera*, *Agapostemon splendens* (Lepeletier) or sweat bee and *Megachile brevis* (Say), a Megachilidae. In the invasive range, Spain, *O. stricta* is visited by honeybees and carpenter bees (*X. violacea*) (Bartomeus and Vilà, 2009; Vilà *et al*, 2009), while in South Africa, Rambuda (2001) found honeybees to be the main pollinators of *O. stricta*.

The behaviour of the stamens or thigomotaxis results in stamens bending towards the style or moving towards a stimulus e.g. when an insect visits (Grant and Hurd, 1979) and has been observed in *Opuntia* species (Reyes-Agüero *et al*, 2006). The stamen movement towards the stimulus either ensures pollen is deposited onto the insect, or the insect rapidly abandons the flower and when alighting on the next flower lands on the stigma instead of the stamens, thereby ensuring pollen deposition and preventing pollen theft (Grant and Hurd, 1979; Sclindwein and Wittmann, 1997; Reyes-Agüero *et al*, 2006). When stigmas move towards the style, it is thought to encourage insects to move along the base of the flower, collecting pollen and then movement along the style results in pollination. The other theory is that insects are only able to collect pollen from the upper anthers, without coming into contact with the stigma (Sclindwein and Wittmann, 1997; Reyes-Agüero *et al*, 2006). This behaviour was observed in all of the *Opuntia* species and *P. aculeata*.

Even the most self-incompatible species, *P. caerulea*, appears to have successfully co-opted local pollinators (honeybees and carpenter bees) which were caught bearing pollen, ensuring successful pollination and seed set. In its native range, it is pollinated by *Xylocopa* species, though long toungued bees and hummingbirds have also been recorded visiting flowers (Amela García and Hoc, 1997; Amela García and Gottsberger, 2009). In South Africa, *P. aculaeata* flowers during the winter months and is mainly visited by honeybees and two species of *Allodapini*, appearing to rely more on vegetative reproduction than outcrossing. Bees, bumble-bees and syrphid flies were observed visiting *P. aculeata* in a greenhouse (Leuenberger, 1986), and Grant and Grant (1979) further suggested *P. aculeata* could either have a generalized pollination syndrome or be bee pollinated.

The poricidal anthers of *S. chrysotrichum* and *S. mauritianum* indicate buzz pollination by bees e.g. *Bombus* and *Xylocopa* species, but are also visited by syrphid flies which mistake the poricidal anthers for pseudantherous flowers (those mimicking dehisced anthers) (Buchmann, 1986; Olckers, 2011). A native bee species in southern Brazil, *Melipona obscurior* (Moure), and the introduced species *A. mellifera* both carried *S. mauritianum* pollen, with *A. mellifera* only carrying *S. mauritianum* pollen occasionally, while *M. obscurior* consistently carried large loads of pollen (Hilgert-Moreira *et al*, 2014). In South Africa, Rambuda (2001) found honeybees are unable to buzz pollinate, but curl around the poricidal anthers, effectively collecting pollen on their legs and body (Rambuda, 2001). Similar behaviour of honeybees was observed in this study on *S. mauritianum* as seen in the video of *S. africanum* (Appendix 1: Supplementary Video 4), with *S. mauritianum* plants also being visited by buzz pollinating *Xylocopa* species. For *S. chrysotrichum, Xylocopa* species were observed sonicating flowers, while *Allodapula* species were caught bearing pollen.

Yucca species are thought to have highly specialized pollination biology (Powell, 1992), yet *Y. aloifolia* had successfully co-opted local honeybees in the Eastern Cape that appear to carry large pollen loads. Yucca moths are known to carry out a complex pollinator service, whereby moths copulate within a *Yucca* flower, upon which the female gathers pollen and flies to another *Yucca* flower. Here she deposits part of the pollen on the stigma of the flower after ovipositing within the ovary (Keeley *et al*, 1984). A female moth may pollinate and oviposite in a single flower multiple times (Addicott and Boa, 1999). Within a week, the eggs hatch and larvae feed off the developing ovules until fruit is mature, after which they bore through the fruit wall and descend to the ground using a silk thread (Keeley *et al*, 1984). *Y. aloifolia* however, is considered an exception to specilaized yucca - yucca moth pollination syndrome as no specific moth pollinator is known and reproduction in its native range appears to be by vegetative means, (Pellmyr, 2003). The lack of oviposition scars and the fact that honeybees had been observed pollinating *Y. aloifolia* flowers in Isreal (Galil, 1969), lead Rentsch (2013) to discover *A. mellifera* (a non native species) is effectivley pollinating *Y. aloifolia* diurnally in its native range. The findings of my study support this, and the behaviour of honeybees on entering the flower was similar - it involved disturbing the stamens, before moving to the the base of the flower, were they would often exit the flower by climbing over the stigma and style (Rentsch, 2013).

Theory suggests successful invader species will have a more generalized pollination system, to easily co-opt local species, compared to highly specialized plants that require a specific pollinator to ensure successful pollination. The invasive plant species investigated in this study were pollinated by generalist pollinators, mainly honeybees. Many plant species require pollinators to facilitate their invasion, and the super-generalist honeybee is known to commonly pollinate invasive plants in both its native and introduced range (Richardson *et al*, 2000a). Rambuda and Johnson (2004) found honey bees to be common pollinators of invasive plants in South Africa, and in Australia, Gross *et al* (2010) found non-native honeybees (*A. mellifera*) were required as pollinators, to ensure successful seed set, in the self-compatible invasive species *Phyla canescens* (Kunth) (or carpet weed), and in Tasmania, the exotic shrub, *Lupinus arboreus* (Sims), a legume, relies on introduced honeybees (and an introduced *Bombus* species) for seed set (Stout *et al*, 2002). In America, the partially self-compatible invasive yellow star-thistle (*Centaurea solstitialis* (L.)) relies on introduced honeybees for seed set (Barthell *et al*, 2001), and the self-incompatible purple loosestrife (*L. salicaria*) also relies on invasive honeybees for its spread (Brown and Mitchell, 2001; Mal *et al*, 1992). The increased abundance and worldwide distribution of honeybees could therefore be aggravating the invasion by alien plants (Richardson *et al*, 2000a).

Overall no major shifts in functional pollinators between native and invasive range was observed, with most pollinators caught being similar to the native range or being from the group of predicted pollinators.

5.3 Into the unknown: are invasive species pollen limitated

Plant invaders are expected to be released from pollen limitation by having favourable traits i.e. autonomous self-pollination and agamospermy, as predicted by Baker's Law. From this study, some invasive plant species do show evidence of pollen limitation. Based on breeding system results *M. azedarach*, *O. aurantiaca*, *O. monacantha*, *S. chrysotrichum* and *S. mauritianum* had similar fruit set for the autonomous self-pollination and self-pollination treatments, suggesting lack of pollen limitation. The lack of pollen limitation can be attributed to their ability to self-pollinate. *A. longifolia*, *O. ficus-indica* and *O. stricta* had significantly different fruit set between the autonomous self-pollination and self-pollination treatments, with lack of pollen limitation being due not to the breeding system of these species but their relationship with co-opted pollinators. *M. azedarach* did however show evidence of pollen limitation with a significant increase in seed set with pollen supplementation. This can be attributed to its ability for autonomous self-pollination. The PLI at the level of friut set did not provide further evidence of this. Based on the PLI at the seed level, *O. monacantha* and *Y. aloifolia* showed evidence of pollen limitation. The remaining 9 species showed no evidence of pollen limitation in fruit and seed set, mostly providing support for my hypothesis that invasive species are pollen limited due to inadequate pollen deposition by native pollinators or due to autonomous self-pollination.

Pollen limitation results in too few fruits and/or seeds being produced (Burd, 1994;

Knight *et al*, 2005), and this can be due to either 'quantity limitation' whereby stigmas receive too few pollen grains to enable adequate fertilization, or 'quality limitation' whereby pollen grains received are of a poor quality e.g. self-pollen (Ashman *et al*, 2004; Parker and Haubensak, 2002). One way for plants to escape pollen limitation is to reduce dependence of pollinators, for example through self-compatibility (Morgan and Wilson, 2005), or being capable of autonomous self-pollination. This releases the plant from the need for a mate or pollen vector, which is especially important during the invasion process when mates and/or pollinator availability may be low (Larson and Barrett, 2000; Parker and Haubensak, 2002). If fruit production from autonomous self-pollination is equal to that of self-pollination, pollen limitation is not expected. Lack of pollen limitation suggests the success of these invasive species could be due to autonomous self-pollination or from successfully co-opting local pollinators as in the case of *P. caerulea* which shows no evidence for autonomous self-pollination but is successfully visited by native honeybees and carpenter bees. Another factor to consider is that these invasive species have all had relatively long establishment period in South Africa allowing them to form persistent, outcrossing populations and as such pollen limitation does not appear to be a barrier to their spread.

Little is known about the degree of pollen limitation for invasive plant species but Baker's law predicts uniparental reproduction helps make plants self-reliant, making invasive plants largely independent of local pollinators, although successfully co-opting pollinators has advantages of ensuring recombination and hence increasing the chances of local adaptation. Few of the invasive plants investigated have evidence of pollen limitation in either their native or introduced range. In Portugal, the invasive range of *A. longifolia*, it was found to be pollen limited when supplementary pollination resulted in greater fruit set and seed to ovule ratio (Correia *et al*, 2014), but in contrast this study found no evidence of pollen limition of *A. longifolia* in South Africa. *O. stricta* showed no evidence of pollen limitation in South Africa in this study, and one by Rambuda and Johnson (2004), and no pollen limitation has been observed in its native or introduced range (Bartomeus and Vilà, 2009; Spears Jr., 1987). The number of studies providing evidence for pollen limitation has increased, but there is also evidence indicating lack of pollen limitation in species, with different mechanisms (e.g. pollinator efficiency, population size and number of co-occurring species) thought to be playing a role (Ashman *et al*, 2004; Burd, 1994; Knight *et al*, 2005).

An initial study showed pollen limitation was observed in an invasive exotic shrub *Cytisus scoparius* ((L.)Link) (Parker, 1997) and further investigation showed sites with lower pollinator visitation i.e. fewer 'tripped flowers' resulted in pollen limitation, while *Genista monspessulana* ((L.)Bolós and Vigo), a co-occurring invasive species, was found to be pollen limited at both sites (Parker and Haubensak, 2002). In Spain, an investigation into pollen limitation in two invasive species showed different results, with *Carpobrotus acinaciformis* ((L.)Bolus) showing pollen limitation with decreases in seed set possibly caused by inefficiency of local pollinators, while *O. stricta* showed no evidence of pollen limitation (Bartomues and Vilà, 2009). Rambuda and Johnson (2004) found that five invasive species in South Africa showed no evidence of being pollen limited at the level of fruit or seed set, and Muñoz and Cavieres (2008) investigated whether the presence of a showy, herbaceous plant *Taraxacum officinale* (Wigg) would affect the seed set of two native Asteraceae *Hypochaeris thrincioides* (Remy) and *Perezia carthamoides* ((D. Don)Hook) in the Chilean Andes. Pollen supplementation experiments showed the two native species to be pollen limited, with the presence of a single *T. officinale* individual in the population not affecting seed set. The presence of five *T. officinale* individuals in the population, however, resulted in a significant decrease in seed set of the two native species. The invasive species *Hakea salicifolia* ((Vent.)B.L.Burtt) was found to be pollen limited in both naturalized and non-naturalized populations in the Western Cape Province of South Africa, though this is not thought to prevent an invasion as this species is capable of reproducing via autonomous self-pollination (Moodley et al, 2015). Experiments on the invasive plant *L. japonica* showed a difference in fruit set between pollen supplementation, naturally pollinated flowers and autonomous self-pollination suggesting this plant is pollen limited in the invasive range (Larson *et al*, 2002). Pollen limitation, however, may not be an important factor to consider for invasive plant species, as pollen limitation can be observed in their native and/or invasive range, and they still manage to survive. This said, the degree of pollen limitation should not only be investigated on a local scale, with Burd (1994) showing that pollen limitation can vary between sites, times and years suggesting longer termed studies between different populations is needed to understand the true degree of pollen limitation in invasive species.

5.4 Growth trials, seed germination and asexual root production by fruit

The mixing of sexual traits such as the production of fruit (dispersal) with asexual reproduction (rapid, clonal growth) to develop well-adapted offspring capable of surviving away from the parent plant is an excellent strategy to ensure successful establishment and persistence away from the mother plant. Fruit can be dispersed away from the parent by birds, mammals or through water action (dispersal along water courses/estuaries). In the case of *O. aurantiaca* any cladode, which becomes dislodged is capable of vegetative reproduction by sending out roots. The development of roots from *Opuntia* cladodes, even after long distance dispersal (including via water), is not new, though growth of roots from fruit is less well documented. An investigation into *O. aurantiaca* in the Eastern Cape mentioned "root tubers" growing from joints and/or fruit (Archibald, 1936); *Opuntia fragilis* ((Nutt.) Haw) cladodes are known to survive for more than 40 days in still water, and still have 86% rooting (Reyes-Agüero *et al*, 2006); and fruit of *O. monacantha* had 100% rooting (Lenzi and Orth, 2012). In *Opuntia* species, even fruit produced via agamospermy (asexual) produced roots and later went on to develop cladodes and hence plants.

Producing viable seeds could ensure successful establishment for an invasive plant species. The emergence of *O. ficus-indica* and *Y. aloifolia* seedlings means seeds could be effectively dispersed by agents (e.g. monkeys for *Opuntia* and birds for *Y. aloifolia*), to establish successful populations away from the parent plant. Only three species were chosen for germination trials as a test to see whether seedlings may be contributing to the spread of these species. Firstly, *O. aurantiaca* was used as it is thought to be a "sterile hybrid" in South Africa, *O. ficus-indica* was used to test for viability of black/brown seeds and germination success of seeds from the control treatment, and *Y. aloifolia*, as little is known about seed viability in South Africa, especially since it is synonymous with the yucca-moth specialization.

Of the fruit collected for *O. aurantiaca*, no black viable seeds were found and the germination trail on seeds yielded no seedlings, results that are supported by Archibald (1936) who found extremely low numbers of viable seeds in *O. aurantiaca* seeds in South Africa. The black seeds of *O. ficus-indica* were found to be viable, and seeds from the control treatment produced numerous seedlings, suggesting these species may not only be relying on vegetative reproduction. Lenzi and Orth (2012) conducted germination trials on *O. monacantha* and showed the control treatment to have the highest germination rate of 76%, followed by cross-pollination (31%), self-pollination (16%) and autonomous self-pollination, with 5% germination (Lenzi and Orth, 2012). In the field however, germination rate was 1.25% for natural pollination and within 24 months no seedlings were found, suggesting 100% seedling mortality (Lenzi and Orth, 2012). Further investigation is therefore required to assess germination success of *O. ficus-indica* seeds in the field. *Y. aloifolia* seed established successfully in the field and greenhouse experiments, and there was little seedling mortality, suggesting they are able to establish populations away from the parent plant. To date, *Yucca aloifolia* has not yet been assigned an invasive status in South Africa. This means the production of fruit with viable seeds in South Africa, which can be dispersed and germinate without the assistance from humans, suggests this species could continue spreading, and should be considered a serious threat.

5.5 Conclusion and practical considerations

The majority of invasive species investigated in this study were capable of uniparental reproduction through autonomous self-pollination or agamospermy. They also manage to co-opted local pollinators in most cases, which appear to be contributing to outcrossing to some degree, with no species showing evidence of pollen limitation at the level of fruit set and only one showing evidence of pollen limitation of seed production. The data from this study therefore shows strong support for the ideas outlined in Baker's Law.

Thus, this study helps to identify traits, which may contribute to predicting the likeliness of other species becoming invasive in the future. The ability to set fruit and/or seed via autonomous self-pollination and co-opt local pollinators, especially honeybees, appears to be synonymous with these invasive species. All species that show the potential for agamospermy, are self-compatible, or are highly generalized with regard to pollination mode should all be included on a ”prohibited” list, which should be easily accessible and known to the general public. The movement of seeds and/or plant material (including cultivars) from these species should be prohibited and this needs to be enforced. South Africans also need to be made more aware of the risks associated with importing unknown species.

Early detection and eradication, while populations are still small and manageable, is the best solution but for some species, like the ones in this study, complete removal from our natural habitats may be unrealistic especially since many of them are well established and adapting to local environments. Finding novel ways to control them using reproductive biology, biocontrol, chemicals, physical removal and/or a combination of these methods might be more practical.

5.5.1 Recommendations

Future studies should include a multidimensional approach, including the following recommendations where possible:

- Identify modes of reproduction by comparing breeding systems, dependence on pollinators and pollen limitation of ‘related’ native plant species and invasive plants between different populations and among species with differing invasion times and at different stages of invasion.

- Studies on reproductive biology should not only focus on the invasive range, but should also include the native range, and this should be done preferably at species level but if that is not possible, at the level of plant genus/family.

- More large-scale studies, which include diverse species, are needed to ascertain were differences lie between species.

- Fruit and seed dispersal, and establishment in the new environment needs to be assessed.

- Genetic evidence should be included in studies as they could provide details such as the source location of the invasive species (especially if it has a broad native range), presence/absence of self-compatibility gene, and whether the particular invasive is all one clone or not.

These traits need to be incoporated into a larger database which includes other life history traits of current invasive plant species. Effective risk assessment of weeds is currently undertaken in Australia (see Weed Risk Assessment process on the Australian Government Department of Agriculture and Water Resources for more infomation) and a similar process could be add to the plan currently used in South Africa.

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Appendix 1

Supplementary Video 1: A short video showing the sonication of *Solanum mauritianum* anthers using a vibrating tuning fork:
https://youtu.be/2Vl0fEvdx6A

Supplementary Video 2: Thigmotrphism or the movement of anthers in response to a stimulus as seen in *Opuntia-ficus indica*:
https://youtu.be/l-24-nTBfto

Supplementary Video 3, A - E: Carpenter bees (*Xylocopa* species) removing nectar from *Passiflora caerulea* flowers, with pollen being deposited on their body:
https://youtu.be/JWY288eH5Do

Supplementary Video 4: *Apis mellifera* (honeybee) removing pollen from *Solanum africanum* anthers by agitating the poricidal anthers with their heads. The same behaviour of honeybees was observed in the invasive *Solanum mauritianum*:
https://youtu.be/Yh8YZe7D2NI

Appendix 2

Plant species locality data for all individuals used in the breeding system, pollen limitation and growth trial experiments for this study.

Plant species	Road	Town/Locality	Co-ordinates		Notes
Acacia longifolia	R67	Stones Hill	33°19'55.81"S	26°34'25.00"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°19'57.31"S	26°34'58.86"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°19'57.41"S	26°34'59.95"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°19'57.58"S	26°35'1.01"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°19'57.66"S	26°35'1.50"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°19'57.76"S	26°35'2.65"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°19'57.78"S	26°35'3.45"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°19'58.13"S	26°35'5.33"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°19'58.31"S	26°35'6.73"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°19'58.56"S	26°35'8.91"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°19'58.83"S	26°35'9.84"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°19'58.83"S	26°35'10.21"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°19'58.90"S	26°35'10.79"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°19'58.87"S	26°35'11.17"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°19'58.94"S	26°35'11.54"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°19'59.02"S	26°35'12.31"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°19'59.30"S	26°35'14.03"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°19'59.28"S	26°35'14.59"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°19'59.45"S	26°35'15.98"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°19'59.47"S	26°35'16.66"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°19'59.90"S	26°35'18.69"E	Road reserve

Acacia longifolia	R67	Stones Hill	33°19'59.93"S	26°35'20.38"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°20'0.30"S	26°35'22.77"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°20'0.32"S	26°35'25.15"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°20'0.27"S	26°35'25.89"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°20'9.10"S	26°38'5.49"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°20'9.36"S	26°38'5.85"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°20'9.51"S	26°38'6.12"E	Road reserve
Acacia longifolia	R67	Stones Hill	33°20'9.56"S	26°38'6.40"E	Road reserve
Melia azedrach	Glastonbury Road	Grahamstown	33°17'55.00"S	26°31'3.24"E	Road reserve
Melia azedrach	Selworthy Road	Grahamstown	33°17'39.82"S	26°30'53.49"E	Road reserve
Melia azedrach	Selworthy Road	Grahamstown	33°17'40.15"S	26°30'52.83"E	Road reserve
Melia azedrach	Highbridge Road	Grahamstown	33°17'31.21"S	26°30'54.41"E	Road reserve
Melia azedrach	Highbridge Road	Grahamstown	33°17'31.04"S	26°30'55.93"E	Road reserve
Melia azedrach	Highbridge Road	Grahamstown	33°17'31.25"S	26°31'2.67"E	Road reserve
Melia azedrach	Cotterill Street	Grahamstown	33°17'29.75"S	26°31'13.58"E	Road reserve
Melia azedrach	Mac Gowan Street	Grahamstown	33°17'32.38"S	26°31'16.30"E	Road reserve
Melia azedrach	Hare Street	Grahamstown	33°18'30.27"S	26°30'41.36"E	Road reserve
Melia azedrach	Hare Street	Grahamstown	33°18'30.48"S	26°30'40.84"E	Road reserve
Melia azedrach	Worcester Street	Grahamstown	33°18'42.87"S	26°30'26.43"E	Road reserve
Melia azedrach	Constitution Street	Grahamstown	33°18'17.24"S	26°31'1.54"E	Road reserve
Melia azedrach	Milner Street	Grahamstown	33°18'13.30"S	26°31'15.77"E	Road reserve
Melia azedrach	Milner Street	Grahamstown	33°18'13.10"S	26°31'15.62"E	Road reserve
Melia azedrach	Miles Street	Grahamstown	33°17'48.76"S	26°31'28.07"E	Road reserve
Melia azedrach	Selborne Road	Grahamstown	33°17'51.81"S	26°31'27.31"E	Road reserve
Melia azedrach	Selborne Road	Grahamstown	33°17'53.21"S	26°31'28.32"E	Road reserve
Melia azedrach	Selborne Road	Grahamstown	33°17'55.39"S	26°31'32.20"E	Road reserve
Melia azedrach	Selborne Road	Grahamstown	33°17'56.74"S	26°31'30.30"E	Road reserve

Melia azedrach	Leicester Street	Grahamstown	33°18'30.55"S	26°30'34.91"E	Road reserve
Melia azedrach	South Street	Grahamstown	33°18'35.89"S	26°30'47.82"E	Road reserve
Melia azedrach	South Street	Grahamstown	33°18'36.24"S	26°30'47.96"E	Road reserve
Melia azedrach	South Street	Grahamstown	33°18'37.27"S	26°30'48.22"E	Road reserve
Melia azedrach	Cartwright Avenue	Grahamstown	33°18'25.00"S	26°30'34.06"E	Road reserve
Melia azedrach	Cartwright Avenue	Grahamstown	33°18'20.22"S	26°30'33.79"E	Road reserve
Melia azedrach	Willshire Crescent	Grahamstown	33°18'14.72"S	26°30'21.70"E	Road reserve
Melia azedrach	Willshire Crescent	Grahamstown	33°18'21.31"S	26°30'30.85"E	Road reserve
Melia azedrach	Willshire Crescent	Grahamstown	33°18'17.63"S	26°30'28.06"E	Road reserve
Melia azedrach	Stanley Louw Street	Grahamstown	33°18'15.40"S	26°30'20.65"E	Road reserve
Melia azedrach	Stanley Louw Street	Grahamstown	33°18'15.32"S	26°30'22.00"E	Road reserve
Melia azedrach	Winford Road	Grahamstown	33°17'37.77"S	26°31'9.44"E	Road reserve
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'29.43"S	26°29'17.86"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'29.55"S	26°29'17.73"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'29.72"S	26°29'17.68"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'29.95"S	26°29'17.57"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'30.35"S	26°29'17.64"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'30.47"S	26°29'17.57"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'30.60"S	26°29'17.66"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'30.71"S	26°29'17.59"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'30.82"S	26°29'17.80"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'30.70"S	26°29'17.76"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'29.96"S	26°29'17.86"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'31.05"S	26°29'17.77"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'30.97"S	26°29'17.65"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'30.40"S	26°29'17.71"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'30.08"S	26°29'17.70"E	Old dump site

Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'30.03"S	26°29'17.57"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'29.91"S	26°29'17.64"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'30.00"S	26°29'17.60"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'30.08"S	26°29'17.63"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'30.14"S	26°29'17.73"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'29.98"S	26°29'17.73"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'31.12"S	26°29'17.71"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'31.23"S	26°29'17.64"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'31.35"S	26°29'17.75"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'30.96"S	26°29'17.89"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'30.88"S	26°29'17.84"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'31.16"S	26°29'17.71"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'31.21"S	26°29'17.77"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'31.30"S	26°29'17.76"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'31.13"S	26°29'17.73"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'30.90"S	26°29'17.74"E	Old dump site
Opuntia aurantiaca	Burnt Kraal	Grahamstown	33°16'30.78"S	26°29'17.82"E	Old dump site
Opuntia ficus-indica	R350	Grahamstown	33°16'11.39"S	26°28'16.50"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°16'13.10"S	26°28'18.88"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°16'13.23"S	26°28'19.22"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°16'14.17"S	26°28'20.57"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°16'15.27"S	26°28'23.23"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°16'17.46"S	26°28'25.54"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°16'17.01"S	26°28'25.95"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°16'20.69"S	26°28'30.46"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°16'36.19"S	26°28'51.66"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°16'36.66"S	26°28'52.28"E	Road reserve

Opuntia ficus-indica	R350	Grahamstown	33°16'38.39"S	26°28'55.53"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°16'40.84"S	26°28'58.34"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°16'43.72"S	26°29'0.66"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°15'56.86"S	26°27'53.76"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°15'52.91"S	26°27'46.50"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°15'54.82"S	26°27'48.69"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°15'55.60"S	26°27'50.16"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°15'56.24"S	26°27'50.98"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°15'56.52"S	26°27'51.73"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°15'56.89"S	26°27'52.49"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°15'55.43"S	26°27'51.12"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°15'55.55"S	26°27'51.52"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°15'58.01"S	26°27'56.04"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°15'58.21"S	26°27'54.44"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°15'50.63"S	26°27'45.55"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°17'15.31"S	26°29'17.78"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°17'19.05"S	26°29'20.60"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°17'18.71"S	26°29'20.46"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°17'19.25"S	26°29'20.80"E	Road reserve
Opuntia ficus-indica	R350	Grahamstown	33°17'18.74"S	26°29'20.01"E	Road reserve
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'29.98"S	26°36'33.66"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'30.05"S	26°36'33.80"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'25.30"S	26°36'31.87"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'25.52"S	26°36'31.89"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'25.27"S	26°36'31.85"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'27.35"S	26°36'37.89"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'27.12"S	26°36'38.87"E	Open veld

Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'21.76"S	26°37'4.02"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'28.41"S	26°36'49.60"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'28.22"S	26°36'45.75"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'26.56"S	26°37'28.97"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'26.30"S	26°37'28.95"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'27.31"S	26°37'27.47"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'26.01"S	26°37'33.33"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'25.20"S	26°37'32.98"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'20.12"S	26°37'37.86"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'20.45"S	26°37'38.16"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'20.69"S	26°37'38.43"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'21.02"S	26°37'38.95"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'21.31"S	26°37'39.62"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'21.84"S	26°37'41.06"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'22.64"S	26°37'42.00"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'22.24"S	26°37'43.37"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'22.65"S	26°37'43.35"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'22.51"S	26°37'44.50"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'22.85"S	26°37'44.88"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'23.32"S	26°37'44.96"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'23.52"S	26°37'45.38"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'23.73"S	26°37'45.82"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'24.18"S	26°37'46.00"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'24.46"S	26°37'46.26"E	Open veld
Opuntia monacantha	Kariega Game Reserve	Kenton-on-sea	33°36'24.74"S	26°37'46.42"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'25.12"S	26°37'31.18"E	Dam wall
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'25.54"S	26°37'32.91"E	Dam wall

Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'25.16"S	26°37'32.59"E	Dam wall
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'27.15"S	26°37'25.97"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'27.10"S	26°37'25.09"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'26.42"S	26°37'24.89"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'25.26"S	26°37'23.11"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'24.97"S	26°37'22.85"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'23.88"S	26°37'21.81"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'23.60"S	26°37'21.79"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'23.27"S	26°37'21.83"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'23.04"S	26°37'21.51"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'24.96"S	26°37'22.15"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'22.03"S	26°37'21.01"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'21.47"S	26°37'20.39"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'20.85"S	26°37'20.68"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'20.26"S	26°37'21.12"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'19.27"S	26°37'19.52"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'19.30"S	26°37'20.05"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'19.64"S	26°37'20.66"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'19.98"S	26°37'22.25"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'20.85"S	26°37'24.71"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'22.05"S	26°37'25.06"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'21.94"S	26°37'25.78"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'22.25"S	26°37'26.08"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'22.48"S	26°37'26.45"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'22.76"S	26°37'27.49"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'22.69"S	26°37'27.70"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'22.50"S	26°37'27.83"E	Open veld

Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'22.23"S	26°37'27.71"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'24.72"S	26°37'25.58"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'24.30"S	26°37'30.62"E	Open veld
Opuntia stricta	Kariega Game Reserve	Kenton-on-sea	33°36'24.75"S	26°37'32.77"E	Open veld
Passiflora caerulea	Mosslands (N2)	Grahamstown	33°23'48.22"S	26°25'6.49"E	Fence/road reserve
Passiflora caerulea	Mosslands (N2)	Grahamstown	33°23'48.15"S	26°25'6.50"E	Fence/road reserve
Passiflora caerulea	Mosslands (N2)	Grahamstown	33°23'48.06"S	26°25'6.42"E	Fence/road reserve
Passiflora caerulea	Mosslands (N2)	Grahamstown	33°23'47.97"S	26°25'6.41"E	Fence/road reserve
Passiflora caerulea	Mosslands (N2)	Grahamstown	33°23'48.00"S	26°25'6.32"E	Fence/road reserve
Passiflora caerulea	Mosslands (N2)	Grahamstown	33°23'47.85"S	26°25'7.21"E	Fence/road reserve
Passiflora caerulea	Mosslands (N2)	Grahamstown	33°23'47.80"S	26°25'7.42"E	Fence/road reserve
Passiflora caerulea	Mosslands (N2)	Grahamstown	33°23'47.78"S	26°25'7.58"E	Fence/road reserve
Passiflora caerulea	Mosslands (N2)	Grahamstown	33°23'47.73"S	26°25'7.73"E	Fence/road reserve
Passiflora caerulea	Mosslands (N2)	Grahamstown	33°23'47.68"S	26°25'7.91"E	Fence/road reserve
Passiflora caerulea	Mosslands (N2)	Grahamstown	33°23'47.68"S	26°25'8.09"E	Fence/road reserve
Passiflora caerulea	Mosslands (N2)	Grahamstown	33°23'47.59"S	26°25'8.28"E	Fence/road reserve
Passiflora caerulea	Mosslands (N2)	Grahamstown	33°23'47.53"S	26°25'8.45"E	Fence/road reserve
Passiflora caerulea	Mosslands (N2)	Grahamstown	33°23'47.46"S	26°25'8.63"E	Fence/road reserve
Passiflora caerulea	Mosslands (N2)	Grahamstown	33°23'47.42"S	26°25'8.82"E	Fence/road reserve
Passiflora caerulea	Mosslands (N2)	Grahamstown	33°23'47.38"S	26°25'8.93"E	Fence/road reserve
Passiflora caerulea	Mosslands (N2)	Grahamstown	33°23'47.34"S	26°25'9.08"E	Fence/road reserve
Passiflora caerulea	Mosslands (N2)	Grahamstown	33°23'47.31"S	26°25'9.23"E	Fence/road reserve
Passiflora caerulea	Mosslands (N2)	Grahamstown	33°23'48.90"S	26°25'6.25"E	Fence/road reserve
Passiflora caerulea	Mosslands (N2)	Grahamstown	33°23'48.86"S	26°25'6.34"E	Fence/road reserve
Passiflora caerulea	Mosslands (N2)	Grahamstown	33°23'48.81"S	26°25'6.47"E	Fence/road reserve
Passiflora caerulea	Mosslands (N2)	Grahamstown	33°23'48.85"S	26°25'6.44"E	Fence/road reserve
Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.22"S	26°31'25.00"E	Creeper

Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.28"S	26°31'24.94"E	Creeper
Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.36"S	26°31'24.91"E	Creeper
Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.40"S	26°31'24.86"E	Creeper
Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.43"S	26°31'24.78"E	Creeper
Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.53"S	26°31'24.65"E	Creeper
Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.56"S	26°31'24.54"E	Creeper
Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.56"S	26°31'24.54"E	Creeper
Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.56"S	26°31'24.44"E	Creeper
Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.51"S	26°31'24.38"E	Creeper
Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.45"S	26°31'24.35"E	Fence/road reserve
Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.47"S	26°31'24.29"E	Fence/road reserve
Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.49"S	26°31'24.23"E	Fence/road reserve
Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.50"S	26°31'24.20"E	Fence/road reserve
Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.58"S	26°31'24.14"E	Fence/road reserve
Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.59"S	26°31'24.08"E	Fence/road reserve
Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.61"S	26°31'24.03"E	Fence/road reserve
Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.63"S	26°31'23.98"E	Fence/road reserve
Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.66"S	26°31'23.90"E	Fence/road reserve
Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.77"S	26°31'23.78"E	Fence/road reserve
Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.79"S	26°31'23.67"E	Fence/road reserve
Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.83"S	26°31'23.53"E	Fence/road reserve
Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.90"S	26°31'23.38"E	Fence/road reserve
Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.14"S	26°31'24.66"E	Fence/road reserve
Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.28"S	26°31'24.50"E	Fence/road reserve
Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.38"S	26°31'24.41"E	Fence/road reserve
Passiflora caerulea	Huntley Street	Grahamstown	33°18'49.10"S	26°31'25.17"E	Fence/road reserve
Passiflora caerulea	Huntley Street	Grahamstown	33°18'48.96"S	26°31'25.08"E	Fence/road reserve

Passiflora caerulea	Leicester Street	Grahamstown	33°18'37.74"S	26°30'23.03"E	Fence/road reserve
Passiflora caerulea	Leicester Street	Grahamstown	33°18'37.64"S	26°30'22.98"E	Fence/road reserve
Passiflora caerulea	Leicester Street	Grahamstown	33°18'37.65"S	26°30'23.11"E	Fence/road reserve
Passiflora caerulea	Leicester Street	Grahamstown	33°18'37.71"S	26°30'23.21"E	Fence/road reserve
Passiflora caerulea	Leicester Street	Grahamstown	33°18'37.56"S	26°30'23.36"E	Fence/road reserve
Passiflora caerulea	Leicester Street	Grahamstown	33°18'37.52"S	26°30'23.36"E	Fence/road reserve
Passiflora caerulea	Leicester Street	Grahamstown	33°18'37.38"S	26°30'23.34"E	Fence/road reserve
Passiflora caerulea	Leicester Street	Grahamstown	33°18'37.33"S	26°30'23.42"E	Fence/road reserve
Passiflora caerulea	Leicester Street	Grahamstown	33°18'37.30"S	26°30'23.44"E	Fence/road reserve
Passiflora caerulea	Leicester Street	Grahamstown	33°18'37.25"S	26°30'23.54"E	Fence/road reserve
Passiflora caerulea	Leicester Street	Grahamstown	33°18'37.21"S	26°30'23.55"E	Fence/road reserve
Passiflora caerulea	Leicester Street	Grahamstown	33°18'37.17"S	26°30'23.63"E	Fence/road reserve
Passiflora caerulea	Leicester Street	Grahamstown	33°18'37.25"S	26°30'23.67"E	Fence/road reserve
Passiflora caerulea	Leicester Street	Grahamstown	33°18'37.76"S	26°30'22.80"E	Fence/road reserve
Passiflora caerulea	Leicester Street	Grahamstown	33°18'37.79"S	26°30'22.73"E	Fence/road reserve
Passiflora caerulea	Leicester Street	Grahamstown	33°18'37.84"S	26°30'22.60"E	Fence/road reserve
Pereskia aculeata	Elizabeth Road	Bathurst	33°29'49.56"S	26°48'52.30"E	Fence/road reserve
Pereskia aculeata	Elizabeth Road	Bathurst	33°29'49.16"S	26°48'53.47"E	Fence/road reserve
Pereskia aculeata	Elizabeth Road	Bathurst	33°29'49.55"S	26°48'52.15"E	Fence/road reserve
Pereskia aculeata	Elizabeth Road	Bathurst	33°29'49.59"S	26°48'52.11"E	Fence/road reserve
Pereskia aculeata	Elizabeth Road	Bathurst	33°29'49.49"S	26°48'52.12"E	Fence/road reserve
Pereskia aculeata	Elizabeth Road	Bathurst	33°29'49.04"S	26°48'53.84"E	Fence/road reserve
Pereskia aculeata	Elizabeth Road	Bathurst	33°29'53.08"S	26°48'47.46"E	Fence/road reserve
Pereskia aculeata	Elizabeth Road	Bathurst	33°29'53.17"S	26°48'47.51"E	Fence/road reserve
Pereskia aculeata	Elizabeth Road	Bathurst	33°29'53.27"S	26°48'47.55"E	Fence/road reserve
Pereskia aculeata	York Road	Bathurst	33°30'15.00"S	26°49'10.82"E	Fence/road reserve
Pereskia aculeata	York Road	Bathurst	33°30'15.10"S	26°49'10.94"E	Fence/road reserve

Pereskia aculeata	Waters Meeting Road	Bathurst	33°30'46.17"S	26°49'4.42"E	Fence/road reserve
Pereskia aculeata	Waters Meeting Road	Bathurst	33°30'46.13"S	26°49'4.72"E	Fence/road reserve
Pereskia aculeata	Waters Meeting Road	Bathurst	33°30'46.03"S	26°49'4.90"E	Fence/road reserve
Pereskia aculeata	Waters Meeting Road	Bathurst	33°30'45.80"S	26°49'5.15"E	Fence/road reserve
Pereskia aculeata	Waters Meeting Road	Bathurst	33°30'45.66"S	26°49'5.35"E	Fence/road reserve
Pereskia aculeata	Waters Meeting Road	Bathurst	33°30'45.47"S	26°49'5.52"E	Fence/road reserve
Pereskia aculeata	Waters Meeting Road	Bathurst	33°30'45.31"S	26°49'5.67"E	Fence/road reserve
Pereskia aculeata	Waters Meeting Road	Bathurst	33°30'45.10"S	26°49'5.94"E	Fence/road reserve
Pereskia aculeata	Waters Meeting Road	Bathurst	33°30'44.99"S	26°49'6.06"E	Fence/road reserve
Pereskia aculeata	Waters Meeting Road	Bathurst	33°30'44.89"S	26°49'6.22"E	Fence/road reserve
Pereskia aculeata	Waters Meeting Road	Bathurst	33°30'44.74"S	26°49'6.36"E	Fence/road reserve
Pereskia aculeata	Waters Meeting Road	Bathurst	33°30'44.59"S	26°49'6.51"E	Fence/road reserve
Pereskia aculeata	Waters Meeting Road	Bathurst	33°30'44.23"S	26°49'6.79"E	Fence/road reserve
Pereskia aculeata	Waters Meeting Road	Bathurst	33°30'43.92"S	26°49'7.21"E	Fence/road reserve
Pereskia aculeata	Waters Meeting Road	Bathurst	33°30'43.77"S	26°49'7.53"E	Fence/road reserve
Pereskia aculeata	Waters Meeting Road	Bathurst	33°30'43.52"S	26°49'7.73"E	Fence/road reserve
Pereskia aculeata	Waters Meeting Road	Bathurst	33°30'43.31"S	26°49'7.90"E	Fence/road reserve
Pereskia aculeata	Waters Meeting Road	Bathurst	33°30'43.04"S	26°49'8.13"E	Fence/road reserve
Pereskia aculeata	Waters Meeting Road	Bathurst	33°30'42.87"S	26°49'8.40"E	Fence/road reserve
Pereskia aculeata	Waters Meeting Road	Bathurst	33°30'42.53"S	26°49'8.78"E	Fence/road reserve
Pereskia aculeata	Waters Meeting Road	Bathurst	33°30'42.40"S	26°49'8.95"E	Fence/road reserve
Pereskia aculeata	Waters Meeting Road	Bathurst	33°30'42.18"S	26°49'9.22"E	Fence/road reserve
Pereskia aculeata	Waters Meeting Road	Bathurst	33°30'41.98"S	26°49'9.55"E	Fence/road reserve
Pereskia aculeata	Waters Meeting Road	Bathurst	33°30'41.65"S	26°49'9.85"E	Fence/road reserve
Pereskia aculeata	Waters Meeting Road	Bathurst	33°30'41.42"S	26°49'10.19"E	Fence/road reserve
Pereskia aculeata	Waters Meeting Road	Bathurst	33°30'41.20"S	26°49'10.39"E	Fence/road reserve
Pereskia aculeata	Prince Alfred Street	Grahamstown	33°18'53.47"S	26°30'45.09"E	Fence/road reserve

Pereskia aculeata	Prince Alfred Street	Grahamstown	33°18'53.51"S	26°30'45.19"E	Fence/road reserve
Pereskia aculeata	Croft Street	Grahamstown	33°18'37.79"S	26°30'43.76"E	Fence/road reserve
Pereskia aculeata	Croft Street	Grahamstown	33°18'37.99"S	26°30'43.82"E	Fence/road reserve
Pereskia aculeata	Croft Street	Grahamstown	33°18'38.14"S	26°30'43.87"E	Fence/road reserve
Pereskia aculeata	Glastonbury Road	Grahamstown	33°17'48.17"S	26°30'58.34"E	Fence/road reserve
Pereskia aculeata	Glastonbury Road	Grahamstown	33°17'48.12"S	26°30'58.35"E	Fence/road reserve
Pereskia aculeata	Glastonbury Road	Grahamstown	33°17'48.07"S	26°30'58.28"E	Fence/road reserve
Pereskia aculeata	Glastonbury Road	Grahamstown	33°17'48.10"S	26°30'58.33"E	Fence/road reserve
Pereskia aculeata	Glastonbury Road	Grahamstown	33°17'48.03"S	26°30'58.33"E	Fence/road reserve
Pereskia aculeata	Glastonbury Road	Grahamstown	33°17'48.26"S	26°30'58.43"E	Fence/road reserve
Pereskia aculeata	Charles Street	Grahamstown	33°18'15.16"S	26°31'29.55"E	Hedge
Pereskia aculeata	Charles Street	Grahamstown	33°18'15.20"S	26°31'29.43"E	Hedge
Pereskia aculeata	Charles Street	Grahamstown	33°18'15.22"S	26°31'29.39"E	Hedge
Pereskia aculeata	Charles Street	Grahamstown	33°18'15.24"S	26°31'29.32"E	Hedge
Pereskia aculeata	Charles Street	Grahamstown	33°18'15.27"S	26°31'29.28"E	Hedge
Pereskia aculeata	Charles Street	Grahamstown	33°18'15.30"S	26°31'29.21"E	Hedge
Pereskia aculeata	Charles Street	Grahamstown	33°18'15.32"S	26°31'29.16"E	Hedge
Pereskia aculeata	Charles Street	Grahamstown	33°18'15.34"S	26°31'29.10"E	Hedge
Pereskia aculeata	Charles Street	Grahamstown	33°18'15.39"S	26°31'29.05"E	Hedge
Pereskia aculeata	Charles Street	Grahamstown	33°18'15.42"S	26°31'28.98"E	Hedge
Pereskia aculeata	Hillsview Road	Grahamstown	33°18'57.05"S	26°31'50.38"E	Hedge
Pereskia aculeata	Hillsview Road	Grahamstown	33°18'57.14"S	26°31'50.47"E	Hedge
Pereskia aculeata	Hillsview Road	Grahamstown	33°18'57.19"S	26°31'50.51"E	Hedge
Pereskia aculeata	Hillsview Road	Grahamstown	33°18'57.28"S	26°31'50.58"E	Hedge
Pereskia aculeata	Hillsview Road	Grahamstown	33°18'57.35"S	26°31'50.63"E	Hedge
Pereskia aculeata	Hillsview Road	Grahamstown	33°18'57.43"S	26°31'50.66"E	Hedge
Pereskia aculeata	Hillsview Road	Grahamstown	33°18'57.47"S	26°31'50.72"E	Hedge

Pereskia aculeata	Lawrance Street	Grahamstown	33°18'57.47"S	26°31'50.77"E	Hedge
Pereskia aculeata	Lawrance Street	Grahamstown	33°18'57.45"S	26°31'50.82"E	Hedge
Pereskia aculeata	Lawrance Street	Grahamstown	33°18'57.43"S	26°31'50.88"E	Hedge
Pereskia aculeata	Lawrance Street	Grahamstown	33°18'57.39"S	26°31'50.97"E	Hedge
Pereskia aculeata	Lawrance Street	Grahamstown	33°18'57.35"S	26°31'51.04"E	Hedge
Pereskia aculeata	Lawrance Street	Grahamstown	33°18'57.32"S	26°31'51.12"E	Hedge
Pereskia aculeata	Lawrance Street	Grahamstown	33°18'57.29"S	26°31'51.16"E	Hedge
Pereskia aculeata	Lawrance Street	Grahamstown	33°18'57.52"S	26°31'50.70"E	Hedge
Pereskia aculeata	Lawrance Street	Grahamstown	33°18'57.48"S	26°31'50.77"E	Hedge
Pereskia aculeata	Hillsview Road	Grahamstown	33°19'8.11"S	26°32'0.15"E	Road reserve
Pereskia aculeata	Hillsview Road	Grahamstown	33°19'8.09"S	26°32'0.34"E	Road reserve
Pereskia aculeata	Hillsview Road	Grahamstown	33°19'8.10"S	26°32'0.45"E	Road reserve
Pereskia aculeata	Hillsview Road	Grahamstown	33°19'8.12"S	26°32'0.67"E	Road reserve
Pereskia aculeata	Hillsview Road	Grahamstown	33°19'8.12"S	26°32'0.87"E	Road reserve
Pereskia aculeata	Hillsview Road	Grahamstown	33°19'8.16"S	26°32'1.13"E	Road reserve
Pereskia aculeata	Hillsview Road	Grahamstown	33°19'8.12"S	26°32'1.26"E	Road reserve
Pereskia aculeata	Hillsview Road	Grahamstown	33°19'8.12"S	26°32'1.45"E	Road reserve
Pereskia aculeata	Hillsview Road	Grahamstown	33°19'8.22"S	26°32'1.70"E	Road reserve
Pereskia aculeata	Hillsview Road	Grahamstown	33°19'8.15"S	26°32'1.82"E	Road reserve
Pereskia aculeata	Hillsview Road	Grahamstown	33°19'8.23"S	26°32'1.99"E	Road reserve
Pereskia aculeata	Hillsview Road	Grahamstown	33°19'8.21"S	26°32'2.23"E	Road reserve
Pereskia aculeata	Hillsview Road	Grahamstown	33°19'8.25"S	26°32'2.45"E	Road reserve
Pereskia aculeata	Hillsview Road	Grahamstown	33°19'8.19"S	26°32'2.62"E	Road reserve
Pereskia aculeata	Huntley Street	Grahamstown	33°18'48.11"S	26°31'26.93"E	Fence/road reserve
Pereskia aculeata	Huntley Street	Grahamstown	33°18'48.23"S	26°31'26.70"E	Fence/road reserve
Pereskia aculeata	Huntley Street	Grahamstown	33°18'48.30"S	26°31'26.49"E	Fence/road reserve
Pereskia aculeata	Huntley Street	Grahamstown	33°18'48.38"S	26°31'26.26"E	Fence/road reserve

Pereskia aculeata	Huntley Street	Grahamstown	33°18'48.51"S	26°31'26.06"E	Fence/road reserve
Pereskia aculeata	Huntley Street	Grahamstown	33°18'48.68"S	26°31'25.75"E	Fence/road reserve
Pereskia aculeata	Huntley Street	Grahamstown	33°18'48.79"S	26°31'25.57"E	Fence/road reserve
Pereskia aculeata	Huntley Street	Grahamstown	33°18'48.95"S	26°31'25.33"E	Fence/road reserve
Pereskia aculeata	Huntley Street	Grahamstown	33°18'49.03"S	26°31'25.11"E	Fence/road reserve
Pereskia aculeata	Huntley Street	Grahamstown	33°18'49.19"S	26°31'24.81"E	Fence/road reserve
Pereskia aculeata	Huntley Street	Grahamstown	33°18'49.36"S	26°31'24.60"E	Fence/road reserve
Pereskia aculeata	Huntley Street	Grahamstown	33°18'49.82"S	26°31'23.54"E	Fence/road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'25.84"S	28°18'14.44"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'26.76"S	28°18'16.39"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'24.88"S	28°18'13.27"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'20.82"S	28°18'11.53"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'20.88"S	28°18'10.93"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'20.54"S	28°18'10.61"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'19.94"S	28°18'10.45"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'19.36"S	28°18'10.23"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'18.87"S	28°18'9.96"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'19.25"S	28°18'10.73"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'11.24"S	28°18'6.23"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'11.77"S	28°18'6.54"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'9.30"S	28°18'4.55"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'9.89"S	28°18'5.01"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'7.46"S	28°18'2.82"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'7.76"S	28°18'3.13"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'6.83"S	28°18'2.22"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°40'49.18"S	28°17'51.24"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°40'21.96"S	28°17'58.73"E	Road reserve

Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°40'21.47"S	28°17'58.87"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°40'27.85"S	28°17'57.77"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°40'28.20"S	28°17'57.70"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'16.19"S	28°18'8.50"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'15.88"S	28°18'8.32"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'15.59"S	28°18'8.11"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'15.31"S	28°18'7.96"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'14.91"S	28°18'7.77"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'14.32"S	28°18'7.29"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'13.74"S	28°18'6.99"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'13.05"S	28°18'6.66"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'12.30"S	28°18'6.25"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'11.63"S	28°18'5.98"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'13.41"S	28°18'7.57"E	Road reserve
Solanum chrysotrichum	George Brown Drive	Morgan Bay	32°41'8.71"S	28°18'3.94"E	Road reserve
Solanum mauritianum	Woest Hill	Grahamstown	33°20'56.01"S	26°33'34.48"E	Road reserve
Solanum mauritianum	Woest Hill	Grahamstown	33°20'56.02"S	26°33'34.72"E	Road reserve
Solanum mauritianum	Woest Hill	Grahamstown	33°20'55.97"S	26°33'36.04"E	Road reserve
Solanum mauritianum	Woest Hill	Grahamstown	33°20'55.86"S	26°33'34.95"E	Road reserve
Solanum mauritianum	Woest Hill	Grahamstown	33°20'55.93"S	26°33'34.49"E	Road reserve
Solanum mauritianum	Woest Hill	Grahamstown	33°20'59.16"S	26°33'36.60"E	Road reserve
Solanum mauritianum	Woest Hill	Grahamstown	33°20'59.28"S	26°33'37.07"E	Road reserve
Solanum mauritianum	Woest Hill	Grahamstown	33°20'26.62"S	26°33'38.55"E	Road reserve
Solanum mauritianum	Woest Hill	Grahamstown	33°20'26.43"S	26°33'38.67"E	Road reserve
Solanum mauritianum	Woest Hill	Grahamstown	33°20'26.28"S	26°33'38.57"E	Road reserve
Solanum mauritianum	Woest Hill	Grahamstown	33°20'26.05"S	26°33'39.15"E	Road reserve
Solanum mauritianum	Leicester Street	Grahamstown	33°18'37.48"S	26°30'23.47"E	Road reserve

Solanum mauritianum	Leicester Street	Grahamstown	33°18'37.70"S	26°30'23.07"E	Road reserve
Solanum mauritianum	Leicester Street	Grahamstown	33°18'38.12"S	26°30'22.58"E	Road reserve
Solanum mauritianum	Worcester Street	Grahamstown	33°18'41.70"S	26°30'26.90"E	Road reserve
Solanum mauritianum	Worcester Street	Grahamstown	33°18'42.18"S	26°30'27.17"E	Road reserve
Solanum mauritianum	Worcester Street	Grahamstown	33°18'41.88"S	26°30'27.99"E	Road reserve
Yucca aloifolia	Worcester Street	Grahamstown	33°18'40.94"S	26°30'30.06"E	Road reserve
Yucca aloifolia	Leicester Street	Grahamstown	33°18'36.01"S	26°30'26.25"E	Road reserve
Yucca aloifolia	Durban Street	Grahamstown	33°18'33.30"S	26°30'48.16"E	Road reserve
Yucca aloifolia	Durban Street	Grahamstown	33°18'33.29"S	26°30'47.97"E	Road reserve
Yucca aloifolia	Durban Street	Grahamstown	33°18'29.27"S	26°30'52.48"E	Road reserve
Yucca aloifolia	Durban Street	Grahamstown	33°18'29.54"S	26°30'51.97"E	Road reserve
Yucca aloifolia	Durban Street	Grahamstown	33°18'29.75"S	26°30'51.60"E	Road reserve
Yucca aloifolia	Durban Street	Grahamstown	33°18'29.92"S	26°30'51.23"E	Road reserve
Yucca aloifolia	Durban Street	Grahamstown	33°18'30.00"S	26°30'51.02"E	Road reserve
Yucca aloifolia	Glastonbury Road	Grahamstown	33°17'48.08"S	26°30'57.99"E	Road reserve
Yucca aloifolia	Glastonbury Road	Grahamstown	33°17'48.12"S	26°30'58.18"E	Road reserve
Yucca aloifolia	Glastonbury Road	Grahamstown	33°17'48.14"S	26°30'58.38"E	Road reserve
Yucca aloifolia	Oatlands Road	Grahamstown	33°18'4.80"S	26°31'11.41"E	Road reserve
Yucca aloifolia	Prince Alfred Street	Grahamstown	33°18'41.24"S	26°31'11.61"E	Road reserve
Yucca aloifolia	Prince Alfred Street	Grahamstown	33°18'41.41"S	26°31'11.75"E	Road reserve
Yucca aloifolia	Rhodes Avenue	Grahamstown	33°18'58.85"S	26°31'5.41"E	Road reserve
Yucca aloifolia	Rhodes Avenue	Grahamstown	33°18'58.84"S	26°31'5.52"E	Road reserve
Yucca aloifolia	Rhodes Avenue	Grahamstown	33°18'58.92"S	26°31'5.60"E	Road reserve
Yucca aloifolia	Rhodes Avenue	Grahamstown	33°18'59.04"S	26°31'5.71"E	Road reserve
Yucca aloifolia	Rhodes Avenue	Grahamstown	33°18'59.19"S	26°31'5.81"E	Road reserve
Yucca aloifolia	Rhodes Avenue	Grahamstown	33°18'59.26"S	26°31'5.90"E	Road reserve
Yucca aloifolia	Rhodes Avenue	Grahamstown	33°18'59.37"S	26°31'5.94"E	Road reserve

Yucca aloifolia	Rhodes Avenue	Grahamstown	33°18'59.22"S	26°31'5.83"E	Road reserve
Yucca aloifolia	Rhodes Avenue	Grahamstown	33°18'59.29"S	26°31'6.02"E	Road reserve
Yucca aloifolia	Lucas Avenue	Grahamstown	33°18'54.43"S	26°31'19.30"E	Road reserve
Yucca aloifolia	Lucas Avenue	Grahamstown	33°18'54.41"S	26°31'19.34"E	Road reserve
Yucca aloifolia	Lucas Avenue	Grahamstown	33°18'54.32"S	26°31'19.47"E	Road reserve
Yucca aloifolia	Lucas Avenue	Grahamstown	33°18'54.39"S	26°31'19.32"E	Road reserve
Yucca aloifolia	West Beach Road	Port Alfred	33°36'8.45"S	26°53'55.99"E	Road reserve
Yucca aloifolia	West Beach Road	Port Alfred	33°36'8.51"S	26°53'56.22"E	Road reserve
Yucca aloifolia	West Beach Road	Port Alfred	33°36'14.62"S	26°53'53.31"E	Road reserve
Yucca aloifolia	West Beach Road	Port Alfred	33°36'14.64"S	26°53'53.34"E	Road reserve
Yucca aloifolia	West Beach Road	Port Alfred	33°36'15.65"S	26°53'46.76"E	Road reserve
Yucca aloifolia	West Beach Road	Port Alfred	33°36'15.55"S	26°53'46.71"E	Road reserve
Yucca aloifolia	West Beach Road	Port Alfred	33°36'15.85"S	26°53'45.61"E	Road reserve
Yucca aloifolia	West Beach Road	Port Alfred	33°36'15.85"S	26°53'45.10"E	Road reserve
Yucca aloifolia	West Beach Road	Port Alfred	33°36'16.83"S	26°53'43.71"E	Road reserve
Yucca aloifolia	West Beach Road	Port Alfred	33°36'16.46"S	26°53'45.13"E	Road reserve
Yucca aloifolia	West Beach Road	Port Alfred	33°36'16.52"S	26°53'45.19"E	Road reserve
Yucca aloifolia	West Beach Road	Port Alfred	33°36'16.38"S	26°53'47.22"E	Road reserve
Yucca aloifolia	West Beach Road	Port Alfred	33°36'16.39"S	26°53'47.28"E	Road reserve
Yucca aloifolia	West Beach Road	Port Alfred	33°36'16.45"S	26°53'47.33"E	Road reserve
Yucca aloifolia	West Beach Road	Port Alfred	33°36'16.25"S	26°53'49.80"E	Road reserve
Yucca aloifolia	West Beach Road	Port Alfred	33°36'16.16"S	26°53'49.66"E	Road reserve
Yucca aloifolia	2nd Avenue	Bushmans River	33°40'48.46"S	26°39'0.87"E	Road reserve
Yucca aloifolia	2nd Avenue	Bushmans River	33°40'48.42"S	26°39'0.85"E	Road reserve
Yucca aloifolia	Seaview Crescent	Cannon Rocks	33°45'0.71"S	26°32'29.27"E	Road reserve
Yucca aloifolia	Seaview Crescent	Cannon Rocks	33°45'0.94"S	26°32'29.38"E	Road reserve
Yucca aloifolia	Seaview Crescent	Cannon Rocks	33°45'1.30"S	26°32'29.45"E	Road reserve

Yucca aloifolia	Alice Road	Cannon Rocks	33°45'4.80"S	26°32'14.57"E	Road reserve
Yucca aloifolia	Alice Road	Cannon Rocks	33°45'4.64"S	26°32'14.93"E	Road reserve
Yucca aloifolia	Second Avenue	Boknes	33°43'44.99"S	26°34'53.72"E	Road reserve
Yucca aloifolia	Second Avenue	Boknes	33°43'35.73"S	26°35'2.82"E	Road reserve
Yucca aloifolia	Second Avenue	Boknes	33°43'35.70"S	26°35'2.92"E	Road reserve
Yucca aloifolia	Second Avenue	Boknes	33°43'48.09"S	26°34'33.56"E	Road reserve
Yucca aloifolia	Daniel Scheepers Road	Boknes	33°43'48.02"S	26°34'33.41"E	Road reserve
Yucca aloifolia	Daniel Scheepers Road	Boknes	33°43'48.05"S	26°34'33.26"E	Road reserve
Yucca aloifolia	Daniel Scheepers Road	Boknes	33°43'48.09"S	26°34'33.13"E	Road reserve
Yucca aloifolia	Daniel Scheepers Road	Boknes	33°43'48.61"S	26°34'34.07"E	Road reserve
Yucca aloifolia	Daniel Scheepers Road	Boknes	33°43'48.92"S	26°34'34.06"E	Road reserve
Yucca aloifolia	Jetty Street	Kenton marina	33°40'46.85"S	26°39'23.57"E	Hedge
Yucca aloifolia	Jetty Street	Kenton marina	33°40'46.79"S	26°39'23.52"E	Hedge
Yucca aloifolia	Jetty Street	Kenton marina	33°40'46.76"S	26°39'23.44"E	Hedge
Yucca aloifolia	Jetty Street	Kenton marina	33°40'46.69"S	26°39'23.32"E	Hedge
Yucca aloifolia	Jetty Street	Kenton marina	33°40'46.58"S	26°39'23.25"E	Hedge
Yucca aloifolia	Jetty Street	Kenton marina	33°40'46.81"S	26°39'23.14"E	Hedge
Yucca aloifolia	Jetty Street	Kenton marina	33°40'46.88"S	26°39'23.21"E	Hedge
Yucca aloifolia	Jetty Street	Kenton marina	33°40'47.01"S	26°39'23.27"E	Hedge
Yucca aloifolia	Jetty Street	Kenton marina	33°40'47.17"S	26°39'23.86"E	Hedge
Yucca aloifolia	Jetty Street	Kenton marina	33°40'47.50"S	26°39'23.57"E	Hedge
Yucca aloifolia	Jetty Street	Kenton marina	33°40'46.29"S	26°39'23.10"E	Hedge
Yucca aloifolia	Jetty Street	Kenton marina	33°40'46.42"S	26°39'22.82"E	Hedge
Yucca aloifolia	Jetty Street	Kenton marina	33°40'46.91"S	26°39'22.95"E	Hedge
Yucca aloifolia	Oetle Street	Kenton-on-sea	33°40'50.58"S	26°40'1.37"E	Road reserve

Appendix 3

Locality data for all insects caught on invasive plants from this study. Exact co-ordinates are not given but locality corresponds with individuals from Appendix 1.

Plant species	**Insect species**	**Town/Locality**	**Date**	**Collector**
Acacia longifolia	*Apis mellifera*	Stones Hill, Grahamstown	24/08/2012	C-J. Thorne
Acacia longifolia	*Apis mellifera*	Stones Hill, Grahamstown	24/08/2012	C-J. Thorne
Acacia longifolia	*Apis mellifera*	Stones Hill, Grahamstown	24/08/2012	C-J. Thorne
Acacia longifolia	*Apis mellifera*	Stones Hill, Grahamstown	24/08/2012	C-J. Thorne
Acacia longifolia	*Apis mellifera*	Stones Hill, Grahamstown	24/08/2012	C-J. Thorne
Acacia longifolia	*Apis mellifera*	Stones Hill, Grahamstown	24/08/2012	C-J. Thorne
Acacia longifolia	*Apis mellifera*	Stones Hill, Grahamstown	24/08/2012	C-J. Thorne
Acacia longifolia	*Apis mellifera*	Stones Hill, Grahamstown	24/08/2012	C-J. Thorne
Acacia longifolia	*Apis mellifera*	Stones Hill, Grahamstown	24/08/2012	C-J. Thorne
Acacia longifolia	*Apis mellifera*	Stones Hill, Grahamstown	19/07/2012	C-J. Thorne
Acacia longifolia	*Apis mellifera*	Stones Hill, Grahamstown	19/07/2012	C-J. Thorne
Acacia longifolia	*Apis mellifera*	Stones Hill, Grahamstown	19/07/2012	C-J. Thorne
Acacia longifolia	*Apis mellifera*	Stones Hill, Grahamstown	18/07/2012	C-J. Thorne
Acacia longifolia	*Apis mellifera*	Stones Hill, Grahamstown	18/07/2012	C-J. Thorne
Acacia longifolia	*Apis mellifera*	Stones Hill, Grahamstown	18/07/2012	C-J. Thorne
Acacia longifolia	*Apis mellifera*	Stones Hill, Grahamstown	18/07/2012	C-J. Thorne
Acacia longifolia	*Apis mellifera*	Stones Hill, Grahamstown	18/07/2012	C-J. Thorne
Acacia longifolia	*Apis mellifera*	Stones Hill, Grahamstown	18/07/2012	C-J. Thorne
Acacia longifolia	*Apis mellifera*	Stones Hill, Grahamstown	18/07/2012	C-J. Thorne

Acacia longifolia	*Apis mellifera*	Stones Hill, Grahamstown	18/07/2012	C-J. Thorne
Acacia longifolia	*Apis mellifera*	Stones Hill, Grahamstown	18/07/2012	C-J. Thorne
Acacia longifolia	*Apis mellifera*	Stones Hill, Grahamstown	18/07/2012	C-J. Thorne
Acacia longifolia	*Asarkina africana*	Stones Hill, Grahamstown	18/07/2012	C-J. Thorne
Acacia longifolia	*Asarkina africana*	Stones Hill, Grahamstown	18/07/2012	C-J. Thorne
Acacia longifolia	*Allodapula*	Stones Hill, Grahamstown	18/07/2012	C-J. Thorne
Acacia longifolia	*Allodape*	Stones Hill, Grahamstown	18/07/2012	C-J. Thorne
Melia azedarach	Diptera	Cartwright Ave, Grahamstown	04/11/2013	C-J. Thorne
Melia azedarach	Chrysomelidae	Cartwright Ave, Grahamstown	04/11/2013	C-J. Thorne
Melia azedarach	*Xylocopa flavicollis*	Highbridge Rd, Grahamstown	25/10/2013	C-J. Thorne
Melia azedarach	Tachinidae	Highbridge Rd, Grahamstown	25/10/2014	C-J. Thorne
Melia azedarach	Tachinidae	Highbridge Rd, Grahamstown	25/10/2015	C-J. Thorne
Melia azedarach	*Apis mellifera*	Selborne Rd, Grahamstown	04/11/2013	C-J. Thorne
Melia azedarach	*Apis mellifera*	Selborne Rd, Grahamstown	04/11/2013	C-J. Thorne
Melia azedarach	*Apis mellifera*	Selborne Rd, Grahamstown	04/11/2013	C-J. Thorne
Melia azedarach	*Apis mellifera*	Selborne Rd, Grahamstown	04/11/2013	C-J. Thorne
Melia azedarach	*Xylocopa flaviocollis*	Selborne Rd, Grahamstown	04/11/2013	C-J. Thorne
Melia azedarach	Noctuidae	Selborne Rd, Grahamstown	04/11/2013	C-J. Thorne
Melia azedarach	*Apis mellifera*	Selborne Rd, Grahamstown	04/11/2013	C-J. Thorne
Melia azedarach	*Apis mellifera*	Selborne Rd, Grahamstown	04/11/2013	C-J. Thorne
Melia azedarach	*Polistes africanus*	Highbridge Rd, Grahamstown	28/10/2013	C-J. Thorne
Melia azedarach	*Polistes africanus*	Highbridge Rd, Grahamstown	28/10/2013	C-J. Thorne
Melia azedarach	Nitidulidae (cf)	Highbridge Rd, Grahamstown	28/10/2014	C-J. Thorne
Melia azedarach	*Crytothyrea marginalis*	Highbridge Rd, Grahamstown	28/10/2015	C-J. Thorne
Melia azedarach	*Xylocopa flaviocollis*	Highbridge Rd, Grahamstown	28/10/2016	C-J. Thorne
Melia azedarach	*Xylocopa flaviocollis*	Highbridge Rd, Grahamstown	28/10/2017	C-J. Thorne
Melia azedarach	*Xylocopa flaviocollis*	Highbridge Rd, Grahamstown	28/10/2018	C-J. Thorne

Melia azedarach	*Xylocopa flaviocollis*	Highbridge Rd, Grahamstown	28/10/2019	C-J. Thorne
Melia azedarach	Cucujoidea	Highbridge Rd, Grahamstown	28/10/2020	C-J. Thorne
Melia azedarach	*Apis mellifera*	Selborne Rd, Grahamstown	29/10/2013	L. Thorne
Melia azedarach	*Apis mellifera*	Selborne Rd, Grahamstown	29/10/2013	L. Thorne
Melia azedarach	*Apis mellifera*	Selborne Rd, Grahamstown	29/10/2013	L. Thorne
Melia azedarach	*Apis mellifera*	Selborne Rd, Grahamstown	29/10/2013	L. Thorne
Melia azedarach	*Apis mellifera*	Selborne Rd, Grahamstown	29/10/2013	L. Thorne
Melia azedarach	*Apis mellifera*	Selborne Rd, Grahamstown	29/10/2013	L. Thorne
Melia azedarach	*Apis mellifera*	Selborne Rd, Grahamstown	29/10/2013	L. Thorne
Melia azedarach	*Apis mellifera*	Selborne Rd, Grahamstown	29/10/2013	L. Thorne
Melia azedarach	*Apis mellifera*	Selborne Rd, Grahamstown	29/10/2013	L. Thorne
Melia azedarach	*Apis mellifera*	Selborne Rd, Grahamstown	29/10/2013	L. Thorne
Melia azedarach	*Xylocopa flavicollis*	Selborne Rd, Grahamstown	29/10/2013	L. Thorne
Melia azedarach	*Xylocopa flavicollis*	Selborne Rd, Grahamstown	29/10/2013	L. Thorne
Melia azedarach	*Xylocopa flavicollis*	Selborne Rd, Grahamstown	29/10/2013	L. Thorne
Melia azedarach	*Xylocopa flavicollis*	Selborne Rd, Grahamstown	29/10/2013	L. Thorne
Melia azedarach	*Xylocopa flavicollis*	Selborne Rd, Grahamstown	29/10/2013	L. Thorne
Melia azedarach	*Xylocopa caffra*	Selborne Rd, Grahamstown	29/10/2013	L. Thorne
Opuntia aurantiaca	*Apis mellifera*	Burnt Kraal, Grahamstown	30/01/2013	C-J. Thorne
Opuntia aurantiaca	*Apis mellifera*	Burnt Kraal, Grahamstown	30/01/2013	C-J. Thorne
Opuntia aurantiaca	*Apis mellifera*	Burnt Kraal, Grahamstown	30/01/2013	C-J. Thorne
Opuntia aurantiaca	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia aurantiaca	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia aurantiaca	*Anthophora wartmanni*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia aurantiaca	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia aurantiaca	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia aurantiaca	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne

Opuntia aurantiaca	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia aurantiaca	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia aurantiaca	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia aurantiaca	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia aurantiaca	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia aurantiaca	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia aurantiaca	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia aurantiaca	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia aurantiaca	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia aurantiaca	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia aurantiaca	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia aurantiaca	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia aurantiaca	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia aurantiaca	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia aurantiaca	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia aurantiaca	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	30/01/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	30/01/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	30/01/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	30/01/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	30/01/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	30/01/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	30/01/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	30/01/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	30/01/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	30/01/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	30/01/2013	C-J. Thorne

Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	30/01/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	30/01/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	30/01/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia ficus-indica	*Apis mellifera*	Burnt Kraal, Grahamstown	01/02/2013	C-J. Thorne
Opuntia monacantha	*Allodape*	Kariega Game Reserve	27/01/2014	N. Klopper
Opuntia monacantha	*Apis mellifera*	Kariega Game Reserve	27/01/2015	N. Klopper
Opuntia monacantha	*Apis mellifera*	Kariega Game Reserve	27/01/2016	N. Klopper
Opuntia monacantha	*Apis mellifera*	Kariega Game Reserve	27/01/2017	N. Klopper
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	28/01/2014	C-J. Thorne
Opuntia stricta	*Allodapula*	Kariega Game Reserve	28/01/2014	C-J. Thorne
Opuntia stricta	*Allodapula*	Kariega Game Reserve	28/01/2014	C-J. Thorne
Opuntia stricta	*Allodape*	Kariega Game Reserve	28/01/2014	C-J. Thorne
Opuntia stricta	*Allodape*	Kariega Game Reserve	28/01/2014	C-J. Thorne
Opuntia stricta	*Allodapula*	Kariega Game Reserve	28/01/2014	C-J. Thorne

Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	28/01/2014	C-J. Thorne
Opuntia stricta	Halictidae Nomia	Kariega Game Reserve	28/01/2014	C-J. Thorne
Opuntia stricta	*Allodape*	Kariega Game Reserve	28/01/2014	C-J. Thorne
Opuntia stricta	*Allodape*	Kariega Game Reserve	28/01/2014	C-J. Thorne
Opuntia stricta	*Allodapula*	Kariega Game Reserve	28/01/2014	C-J. Thorne
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	28/01/2014	C-J. Thorne
Opuntia stricta	*Allodape*	Kariega Game Reserve	28/01/2014	N. Klopper
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	28/01/2014	N. Klopper
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	28/01/2014	N. Klopper
Opuntia stricta	*Allodapula*	Kariega Game Reserve	28/01/2014	N. Klopper
Opuntia stricta	*Allodape*	Kariega Game Reserve	28/01/2014	N. Klopper
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	28/01/2014	N. Klopper
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	28/01/2014	N. Klopper
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	28/01/2014	N. Klopper
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	28/01/2014	N. Klopper
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	28/01/2014	N. Klopper
Opuntia stricta	*Allodapula*	Kariega Game Reserve	27/01/2014	N. Klopper
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	27/01/2014	N. Klopper
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	27/01/2014	N. Klopper
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	27/01/2014	N. Klopper
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	27/01/2014	N. Klopper
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	27/01/2014	N. Klopper
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	27/01/2014	N. Klopper
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	27/01/2014	N. Klopper
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	27/01/2014	N. Klopper
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	27/01/2014	N. Klopper
Opuntia stricta	*Allodapula*	Kariega Game Reserve	27/01/2014	N. Klopper

Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	27/01/2014	N. Klopper
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	26/01/2014	C-J. Thorne
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	26/01/2014	C-J. Thorne
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	26/01/2014	C-J. Thorne
Opuntia stricta	*Allodape*	Kariega Game Reserve	26/01/2014	C-J. Thorne
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	26/01/2014	C-J. Thorne
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	26/01/2014	C-J. Thorne
Opuntia stricta	Meloidae	Kariega Game Reserve	26/01/2014	C-J. Thorne
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	26/01/2014	C-J. Thorne
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	26/01/2014	C-J. Thorne
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	26/01/2014	C-J. Thorne
Opuntia stricta	*Apis mellifera*	Kariega Game Reserve	26/01/2014	C-J. Thorne
Passiflora caerulea	*Xylocopa flavicollis*	Rhodes Transport Dept, Grahamstown	12/09/2012	C-J. Thorne
Passiflora caerulea	*Apis mellifera*	Rhodes Transport Dept, Grahamstown	12/09/2012	C-J. Thorne
Passiflora caerulea	Allodape	Rhodes Transport Dept, Grahamstown	12/09/2012	C-J. Thorne
Passiflora caerulea	*Apis mellifera*	Rhodes Transport Dept, Grahamstown	12/09/2012	C-J. Thorne
Passiflora caerulea	*Apis mellifera*	Rhodes Transport Dept, Grahamstown	12/09/2012	C-J. Thorne
Passiflora caerulea	*Apis mellifera*	Mosslands (N2), Grahamstown	26/11/2012	C-J. Thorne
Passiflora caerulea	*Apis mellifera*	Mosslands (N2), Grahamstown	26/11/2012	C-J. Thorne
Passiflora caerulea	*Apis mellifera*	Mosslands (N2), Grahamstown	26/11/2012	C-J. Thorne
Passiflora caerulea	*Apis mellifera*	Mosslands (N2), Grahamstown	10/12/2012	C-J. Thorne
Passiflora caerulea	*Apis mellifera*	Mosslands (N2), Grahamstown	10/12/2012	C-J. Thorne
Passiflora caerulea	*Apis mellifera*	Mosslands (N2), Grahamstown	10/12/2012	C-J. Thorne
Passiflora caerulea	*Xylocopa flavicollis*	Firtree St, Grahamstown	13/11/2013	C-J. Thorne
Passiflora caerulea	*Apis mellifera*	Huntley St, Grahamstown	13/11/2013	C-J. Thorne
Passiflora caerulea	*Apis mellifera*	Huntley St, Grahamstown	13/11/2013	C-J. Thorne
Passiflora caerulea	*Apis mellifera*	Huntley St, Grahamstown	13/11/2013	C-J. Thorne

Passiflora caerulea	*Apis mellifera*	Huntley St, Grahamstown	13/11/2013	C-J. Thorne
Passiflora caerulea	*Apis mellifera*	Huntley St, Grahamstown	13/11/2013	C-J. Thorne
Passiflora caerulea	*Xylocopa flavorufa*	Huntley St, Grahamstown	13/11/2013	C-J. Thorne
Passiflora caerulea	*Apis mellifera*	Firtree St, Grahamstown	13/11/2013	M. Wolmerans
Passiflora caerulea	*Xylocopa caffra*	Rhodes Transport Dept, Grahamstown	12/09/2012	C-J. Thorne
Pereskia aculeata	*Apis mellifera*	Hillsview Rd, Grahamstown	13/05/2013	C-J. Thorne
Pereskia aculeata	*Apis mellifera*	Hillsview Rd, Grahamstown	13/05/2013	C-J. Thorne
Pereskia aculeata	*Apis mellifera*	Hillsview Rd, Grahamstown	13/05/2013	C-J. Thorne
Pereskia aculeata	*Apis mellifera*	Hillsview Rd, Grahamstown	13/05/2013	C-J. Thorne
Pereskia aculeata	*Apis mellifera*	Hillsview Rd, Grahamstown	13/05/2013	C-J. Thorne
Pereskia aculeata	*Apis mellifera*	Hillsview Rd, Grahamstown	13/05/2013	C-J. Thorne
Pereskia aculeata	*Apis mellifera*	Hillsview Rd, Grahamstown	13/05/2013	C-J. Thorne
Pereskia aculeata	*Apis mellifera*	Hillsview Rd, Grahamstown	13/05/2013	C-J. Thorne
Pereskia aculeata	*Apis mellifera*	Hillsview Rd, Grahamstown	13/05/2013	C-J. Thorne
Pereskia aculeata	*Apis mellifera*	Hillsview Rd, Grahamstown	13/05/2013	C-J. Thorne
Pereskia aculeata	*Apis mellifera*	Hillsview Rd, Grahamstown	13/05/2013	C-J. Thorne
Pereskia aculeata	*Apis mellifera*	Hillsview Rd, Grahamstown	13/05/2013	C-J. Thorne
Pereskia aculeata	*Apis mellifera*	Hillsview Rd, Grahamstown	13/05/2013	C-J. Thorne
Pereskia aculeata	*Apis mellifera*	Hillsview Rd, Grahamstown	13/05/2013	C-J. Thorne
Pereskia aculeata	*Apis mellifera*	Hillsview Rd, Grahamstown	13/05/2013	C-J. Thorne
Pereskia aculeata	*Apis mellifera*	Hillsview Rd, Grahamstown	13/05/2013	C-J. Thorne
Pereskia aculeata	*Apis mellifera*	Hillsview Rd, Grahamstown	13/05/2013	C-J. Thorne
Pereskia aculeata	Allodapula	Hillsview Rd, Grahamstown	13/05/2013	C-J. Thorne
Solanum chrysotrichum	Allodapula	George Brown Dr, Morgan Bay	05/10/2013	C-J. Thorne
Solanum chrysotrichum	Allodapula	George Brown Dr, Morgan Bay	05/10/2013	C-J. Thorne
Solanum chrysotrichum	Melyrides (cf)	George Brown Dr, Morgan Bay	05/10/2013	C-J. Thorne
Solanum mauritianum	*Xylocopa caffra*	Worcester St, Grahamstown	24/04/2012	C-J. Thorne

Solanum mauritianum	*Xylocopa flavorufa*	Worcester St, Grahamstown	24/04/2012	C-J. Thorne
Solanum mauritianum	*Xylocopa flavicollis*	Worcester St, Grahamstown	24/04/2012	C-J. Thorne
Solanum mauritianum	*Xylocopa flavorufa*	Worcester St, Grahamstown	24/04/2012	C-J. Thorne
Solanum mauritianum	*Xylocopa flavicollis*	Worcester St, Grahamstown	24/04/2012	C-J. Thorne
Solanum mauritianum	*Dejeania bombylans*	Worcester St, Grahamstown	21/04/2012	C-J. Thorne
Solanum mauritianum	*Apis mellifera*	Worcester St, Grahamstown	21/04/2012	C-J. Thorne
Solanum mauritianum	*Apis mellifera*	Worcester St, Grahamstown	29/04/2012	C-J. Thorne
Solanum mauritianum	*Apis mellifera*	Worcester St, Grahamstown	24/04/2012	C-J. Thorne
Solanum mauritianum	*Apis mellifera*	Worcester St, Grahamstown	29/04/2012	C-J. Thorne
Solanum mauritianum	*Apis mellifera*	Worcester St, Grahamstown	29/04/2012	C-J. Thorne
Solanum mauritianum	*Apis mellifera*	Worcester St, Grahamstown	24/04/2012	C-J. Thorne
Solanum mauritianum	*Apis mellifera*	Worcester St, Grahamstown	24/04/2012	C-J. Thorne
Solanum mauritianum	*Apis mellifera*	Worcester St, Grahamstown	21/04/2012	C-J. Thorne
Solanum mauritianum	*Apis mellifera*	Worcester St, Grahamstown	21/04/2012	C-J. Thorne
Solanum mauritianum	*Allodapula*	Worcester St, Grahamstown	24/04/2012	C-J. Thorne
Solanum mauritianum	*Apis mellifera*	Worcester St, Grahamstown	24/04/2012	C-J. Thorne
Solanum mauritianum	*Allodapula*	Woest Hill, Grahamstown	25/05/2012	C-J. Thorne
Solanum mauritianum	*Allodapula*	Woest Hill, Grahamstown	25/05/2012	C-J. Thorne
Solanum mauritianum	*Apis mellifera*	Worcester St, Grahamstown	24/04/2012	C-J. Thorne
Solanum mauritianum	*Apis mellifera*	Worcester St, Grahamstown	24/04/2012	C-J. Thorne
Solanum mauritianum	*Xylocopa flavicollis*	Worcester St, Grahamstown	24/04/2012	C-J. Thorne
Solanum mauritianum	*Xylocopa caffra*	Worcester St, Grahamstown	24/04/2012	C-J. Thorne
Solanum mauritianum	*Xylocopa caffra*	Bond St, Grahamstown	16/08/2014	C-J. Thorne
Solanum mauritianum	*Xylocopa flavorufa*	Bond St, Grahamstown	16/08/2014	C-J. Thorne
Solanum mauritianum	*Xylocopa caffra*	Bond St, Grahamstown	16/08/2014	C-J. Thorne
Solanum mauritianum	*Apis mellifera*	Bond St, Grahamstown	16/08/2014	C-J. Thorne
Solanum mauritianum	*Apis mellifera*	Bond St, Grahamstown	16/08/2014	C-J. Thorne

Solanum mauritianum	*Apis mellifera*	Bond St, Grahamstown	16/08/2014	C-J. Thorne
Solanum mauritianum	*Xylocopa flavorufa*	Bond St, Grahamstown	16/08/2014	C-J. Thorne
Solanum mauritianum	*Apis mellifera*	Bond St, Grahamstown	16/08/2014	C-J. Thorne
Solanum mauritianum	*Apis mellifera*	Bond St, Grahamstown	16/08/2014	C-J. Thorne
Yucca aloifolia	*Apis mellifera*	Lucas Ave, Grahamstown	02/04/2014	C-J. Thorne
Yucca aloifolia	*Apis mellifera*	Lucas Ave, Grahamstown	31/03/2014	C-J. Thorne
Yucca aloifolia	*Apis mellifera*	Wood street, PA	24/01/2014	C-J. Thorne
Yucca aloifolia	*Apis mellifera*	Wood street, PA	24/01/2014	C-J. Thorne
Yucca aloifolia	*Apis mellifera*	Lucas Ave, Grahamstown	17/02/2014	C-J. Thorne
Yucca aloifolia	*Apis mellifera*	Rhodes Law Dept, Grahamstown	28/03/2014	C-J. Thorne
Yucca aloifolia	*Apis mellifera*	Lucas Ave, Grahamstown	27/03/2014	C-J. Thorne
Yucca aloifolia	*Apis mellifera*	Glastonbury way, Grahamstown	26/03/2014	C-J. Thorne
Yucca aloifolia	*Apis mellifera*	Glastonbury way, Grahamstown	26/03/2014	C-J. Thorne
Yucca aloifolia	*Apis mellifera*	Glastonbury way, Grahamstown	26/03/2014	C-J. Thorne
Yucca aloifolia	*Apis mellifera*	Beach Rd, Port Alfred	19/01/2014	C-J. Thorne
Yucca aloifolia	*Apis mellifera*	Beach Rd, Port Alfred	19/01/2014	C-J. Thorne
Yucca aloifolia	*Apis mellifera*	Beach Rd, Port Alfred	19/01/2014	C-J. Thorne
Yucca aloifolia	*Apis mellifera*	Beach Rd, Port Alfred	19/01/2014	C-J. Thorne
Yucca aloifolia	*Apis mellifera*	Beach Rd, Port Alfred	19/01/2014	C-J. Thorne