Marram grass seed ecology: the nature of the seed bank and secondary dispersal

Daniel Lim

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Abstract

Marram Grass (*Ammophila arenaria*), represents a significant threat to the natural values of dune systems in southern New Zealand. Following introduction, marram grass' primary mode of invasive spread is vegetative. Key studies suggest that sexual reproduction is of lesser importance (Huiskes, 1979; Hertling and Lubke, 1999; Krajnyk and Maun, 1982). In southern New Zealand, observational evidence suggests that seed may play a much more important role in the invasion of marram grass than has been previously thought. This study therefore has two objectives relating to marram grass seed ecology: 1) to investigate the role of secondary seed dispersal in marram invasion in transgressive dune systems; and 2) to determine if marram grass forms viable seed banks in southern New Zealand. The investigation of secondary seed dispersal was investigated along three lines of enquiry.

Seed production was estimated for flowering populations of marram grass in six depositional environments at Mason Bay, Stewart Island. This aimed to identify those environments that are important sources of invasion and the potential for invasion via seed. The greatest seed production was found in the exposed populations of the northern and backdune nabkha (17,382.5 and 17,772 seeds m^{-2} respectively). The lowest production was found in the semi-stabilised and moribund populations on the trailing arms and coppice dunes (196.5 and 39.4 seeds m^{-2} respectively). Seed production may be related to the input of fresh sand.

Understanding which factors affect germination and emergence in marram grass seed was a key factor in the first objective of the study. The effects of light and darkness and burial appeared to play a major role in determining germination. Marram grass seed was shown to be highly sensitive to light and failed to emerge from depths greater than 5 cm.The restriction of light penetration with increasing burial may be the main factor inhibiting germination in marram grass seed.

Marram grass seedling distribution data was compared against dune environments at Mason Bay. Previous literature suggests that the deflation surfaces (i.e. stonefields) would provide ideal microsites for emergence of seedlings by increasing soil moisture and protecting from micro-erosion. Analysis of seedling distribution however showed a greater proportion of seedlings concentrated outside of deflation surfaces (68.26%) compared to within (31.74%). This finding may be due to the high rainfall experienced at Mason Bay, the eroding nature of the deflation surfaces or the greater overall area of sandsheets.

A unique opportunity was taken to age the marram grass seed bank in two dune systems in southern New Zealand. Viable seed recovered from St Kilda and Allan's Beach was aged between 0 to 21+ years old. The longest previous estimate of marram grass seed bank longevity is 'at least 9 years', making this result particularly significant. The marram grass seed bank may therefore represent a significant threat of re-invasion following control on the foredune.

The final outcomes of this research are a conceptual model of invasion by marram grass seed and management recommendations for ongoing and future marram grass control operations. The entire invasion process is expected to take between six to nine years. Empirical information relating to some aspects of marram grass invasion ecology is currently unavailable and is therefore a key area of future research. Future control operations need to monitor the foredune at least 21 years following eradication and bi-annual systematic searches are required to prevent the establishment and flowering of any new seedlings.

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Chapter 1

Introduction

1.1 Overview

Marram grass (*Ammophila arenaria*) was originally introduced to halt the movement of sand and has had a serious impact on the biodiversity and landform diversity of New Zealand's dune systems. Eradication of marram grass is currently underway in some of New Zealand's nationally and internationally significant dune systems, to preserve their natural character (Hilton and Konlechner, 2010). In order to effectively eradicate this species from the coastal environment, it is important to understand the process of marram grass invasion.

In New Zealand, research has been conducted on the impact of marram grass on the geomorphology and plant assemblages of the dune systems (Dixon et al., 2004; Hilton et al., 2005, 2006, 2009; Partridge, 1995). Studies have has also focused on the process of marram grass invasion at Mason Bay, Stewart Island (Hilton, 2006; Jul et al., 1999), however the exact mechanisms for invasion were not examined. There is a paucity of information relating to seed ecology, in both New Zealand and overseas, with few studies focusing on this key aspect of marram grass invasion (e.g. Huiskes, 1977; Laing, 1958; Pope, 2005). This is despite an abundance of observational evidence collected from eradication operations in southern New Zealand.

The current study therefore investigates key aspects of marram grass seed ecology in order to better understand how marram grass invades dune systems in southern New Zealand. This research will provide valuable empirical evidence relating to different aspects of seed ecology where information has previously been lacking. This is aimed to inform coastal land managers in future eradication operations and provide directions for future research.

1.2 Introduction to invasive weeds

1.2.1 Invasive weeds

The increasingly global movement of humans has allowed for the breakdown of major geographic barriers, such as mountains and oceans, which have historically separated the floras of different continents (Bridges, 1995; Mooney and Hobbs, 2000). This breakdown has lead to the introduction and subsequent naturalisation of many alien plant species. Environmental weeds or ‘invasive plants’ are those introduced plant species that diminish the natural values of an invaded area and cause major modifications to indigenous biodiversity and ecosystem function (Cronk and Fuller, 1995; Williams, 1997; Williams and West, 2000).

1.2.2 Impacts of invasive weeds

Invasive plants can have serious impacts on recipient communities including economic and agronomic loss (Naylor, 2000), displacement of indigenous flora (Hilton *et al.*, 2005; Walls, 1998), the alteration of disturbance regimes and geomorphological processes (Blossey, 1999; Hesp, 2002), the loss of significant habitat of native fauna (Moore and Davis, 2004) and the decrease of local biodiversity (Barbour *et al.*, 1976; Slobodchikoff and Doyen, 1977). In ecosystems, invasive plants can influence species composition and structure, flow of energy and nutrients between vegetation and soil, the susceptibility of vegetation to disturbances, extent of native communities, and rate of recruitment in threatened plants (Owen, 1996; Timmins, 1997; Williams, 1997).

1.2.3 Ideal characteristics of a weed

Studies have attempted to identify those traits, which increase a plant species’ ability to invade into novel environments (Baker, 1965; Hertling and Lubke, 2000; Rejmanék and Richardson, 1996; Sakai *et al.*, 2001). Baker (1965) developed a comprehensive list of ‘ideal weed’ characteristics that are likely to increase the invasive potential of a plant species (Table 1.1). These often reflect adaptations of pioneer species which have a short generation time, high fecundity, fast growth rates and are adapted well to highly disturbed environments (Grime, 1979; Sakai *et al.*, 2001). Traits such as these are important in determining a plant species invasive potential and could be termed ‘ideal’ traits for rapid colonisation and range expansion.

Table 1.1: The attributes of the ‘ideal weed’ adapted from Baker (1965, pp 166) and Hertling and Lubke (2000).

Ideal weed characteristics
Has no special environmental requirements for germination
Has discontinuous germination (self-controlled) and high seed longevity
Shows rapid seedling growth
Spends only a short period of time in the vegetative condition before beginning to flower
Maintains a continuous seed production as long as the growth season permits
Is self-compatible, but not obligatorily self-pollinated
When cross-pollinated, this can be achieved by a non-special flower visitor or by wind
Has very high seed output in favourable environmental conditions
Can produce some seed in a wide range of environmental circumstances – a high tolerance of climatic variation
Has special adaptations for both long and short distance dispersal
Has vigorous vegetative reproduction
Has brittleness at the lower nodes of rhizomes or rootstocks
Shows an ability to regenerate from severed portions of rootstock
Has the ability to compete by special means: rosette formation, choking growth etc

The structure and dynamics of the host environment also plays a key role in determining the success of an invasion (Hobbs and Humphries, 1995). Disturbance is considered to be a major factor affecting the invasibility of natural ecosystems (Hobbs and Huenneke, 1992; Rejmanék, 1989). Although disturbance regimes are a natural aspect of communities, regular disturbances can open up niches for the invasion of weedy species into vulnerable communities. One such community, particularly vulnerable to invasion by weedy plant species because of its large-scale and frequent disturbance regime, is the coastal dune system of New Zealand.

1.2.4 The coastal environment's vulnerability to invasion

The micro-environmental conditions of different soil habitats are influenced by prevailing vegetation, aspect, soil texture, soil colour and other variables that influence incoming and outgoing solar energy (Maun, 2009). In coastal environments, variability in these factors is particularly pronounced due to shifting substrate and lack of shading by plants. These factors also work in concert with other factors such as catastrophic micro-erosion, high diurnal temperature ranges, inundation by seawater, little to no organic matter and extreme moisture deficits to create a frequently disturbed and hostile coastal dune environment (Chapman, 1964; Huiskes, 1979; Salisbury, 1952).

Disturbance has been shown to facilitate the establishment of new species by creating openings for colonisation (Fox and Fox, 1986; Burke and Grime, 1996). Moreno-Casasola (1986) found that species richness decreased with increasing sand movement resulting in a relative lack of native dune species. This increases the invasibility of dune systems by opening up potential opportunities for pioneering invasive plant species that are well-adapted to these difficult conditions. In New Zealand dune systems, there are only three indigenous foredune species, *Poa billardierei*, *Spinifex sericeus* and Pingao (*Ficinia spiralis*) (Partridge, 1995). This lack of species diversity within the active dune environment reduces competition, making it easier for exotic species to establish. One such species is marram grass which has become a significant coastal pest and whose invasion has resulted in alterations to much of the biodiversity and landform diversity of New Zealand's coastal dune systems (Hilton *et al.*, 2005, 2006).

1.3 Marram Grass (*Ammophila arenaria*)

1.3.1 The introduction of marram grass

Marram grass is a dune species native to the coastal regions of Europe, ranging between 63°N and 30°W (Figure 1.1), where it is abundant and often the only species on mobile and semi-mobile dune systems (de la Peña *et al.*, 2009; Schmalzer and Hinkle, 1987). Introduced on a global scale, it has been planted extensively for the stabilisation of dune systems in countries such as North America, Australia, New Zealand and South Africa (Bell, 1988; Buell *et al.*, 1995; Hilton *et al.*, 2000; Lubke *et al.*, 1995; Pickart and Sawyer, 1998). This is largely a result of marram grass' utility as a sand binder, where it can establish on an unstable platform, in freely draining and low nutrient environments such as the foredune (Huiskes, 1979).

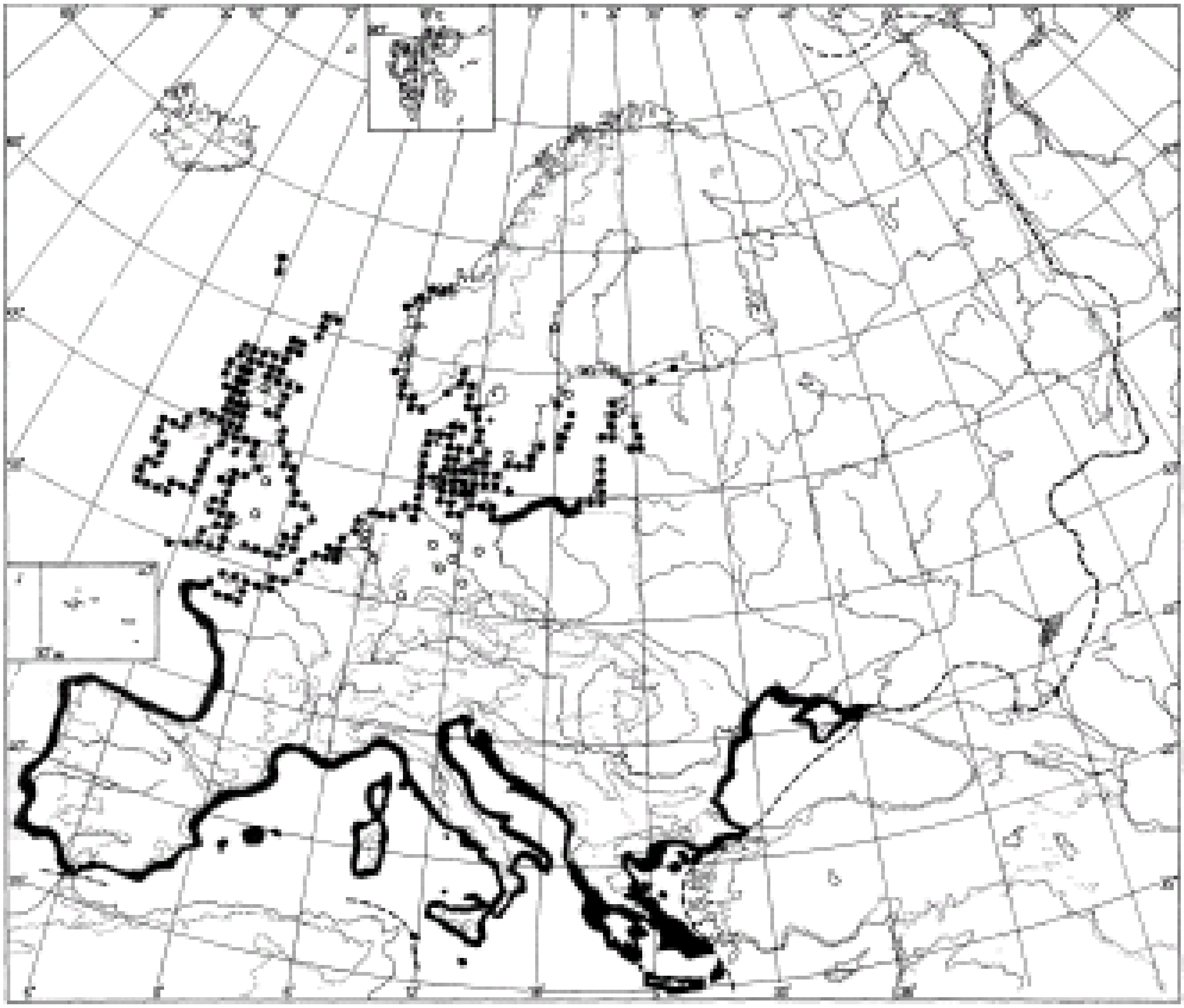

Figure 1.1: The natural extent of marram grass in its European home range. *Source*: Huiskes (1979).

1.3.2 General ecology

Marram grass is a tall, perennial, tussock-like grass which produces dense and extensive networks of rhizomes (Kent *et al.*, 2001; Russo *et al.*, 1988). Inflorescences are initiated in autumn of the second year after germination and mature during summer, with flowering and seed setting occurring between November and March in the southern hemisphere (Pope, 2005). Marram grass has a strong dominance in association with heavily-accreting parts of the dunes however this is reduced in less mobile successional stages of dune and vegetation community development (Carey and Oliver, 1918). As marram grass declines in vigour and abundance on increasingly stable dunes, it becomes shorter, its leaves are less tightly rolled and inflorescences are often absent (Huiskes, 1979; Marshall, 1965). This phenomenon has been related to pathogenic attack of the roots (Van der Putten *et al.*, 1988), failure in the production of new adventitious roots (Maun, 2009), competition from other species better adapted to stable environments; and the reduction in supply of nutrient-providing sand (Marshall, 1965).

1.3.3 Vegetative reproduction

One significant characteristic of marram grass is the production of large numbers of vegetative propagules which facilitate the rapid colonisation of un-invaded coastal dune systems (Radosevich *et al.*, 2007). Marram grass has a particularly strong vegetative strategy with vigorous vegetative reproduction, brittle lower nodes of rhizomes and an ability to regenerate from severed rootstock (Table 1.1) (Hilton *et al.*, 2005; Huiskes, 1979). In a study conducted by Wallen (1980) at Sandhammaren, Skåne, Sweden, an abundance of rhizome fragments from adjacent eroded coasts were washed ashore. Although marram grass is native to the coasts of Europe, this highlights its ability to spread unaided between coastal dune systems, given correct oceanic conditions. In its highly disturbed foredune environment, marram grass rhizome is also often entrained in oceanic currents following scarping of the foredune during storm events. This releases a multitude of vegetative propagules which are able to disperse via water to previously un-invaded dune systems (Konlechner, 2008; Milton, 2004).

The ecological importance of storm-dispersed propagules to marram grass is perhaps best described in Aptekar and Rejmanék’s (2000) study. Once released, marram grass rhizome fragments can be dispersed over long distances depending on ocean currents and the viability of fragments during saltwater transport. Aptekar and Rejmanék (2000) calculated that potential rhizome transportation of 4.3 - 38.9km per day was possible based on near-shore currents along the coast of America's Pacific Northwest. This was coupled with 50% rhizome viability retention after one week's submergence in saltwater and 8.5% viability after 13 days, presenting a maximum travel distance of 505.4km under these conditions. This highlights the significant invasive threat that vegetative dispersal in marram grass poses.

1.3.4 Invasive impacts

Marram grass has been shown to be a highly invasive species in New Zealand, Australia and North America (Bell, 1988; Hilton *et al.*, 2006; Johnson, 1982; Wiedemann and Pickart, 1996). Buell *et al.* (1995) in their investigation into the invasive patterns of marram grass at North Spit, Humboldt Bay, Northern California, found three patterns which reflect marram grass invasion: 1) marram grass spreads rapidly through the foredunes despite not being planted there; 2) marram grass cover increased substantially after 1962, especially after foredune invasion; and 3) marram grass cover on the North Spit increased exponentially over time. Between 1939 and 1989 marram grass cover increased in area by 574% (50ha to 197ha), representing a significant invasive impact. It was proposed that this relatively rapid invasion of the foredune was due to the presence of optimal habitat, natural and human disturbance, multiple introductions into the surrounding area and the proximity of the invaded area to the zone in which fragmented rhizome is washed ashore.

Barbour *et al.* (1976), in their study of coastal vegetation communities between central Washington and the Mexican border (approximately 47 – 33 N°), found that marram grass had a significant impact on the vegetation communities where it had invaded. Overall, species diversity and vegetation cover were negatively correlated with increasing marram grass cover, where it eliminated some species and depressed others. North of 38°N it exerted the most control over community composition compared to any other species. Along the central Oregon coast, marram grass introduction some 136 years previously has resulted in the development of a high, wide foredune, where it was thought none existed before (Wiedemann and Pickart, 1996). Although, it was determined that marram grass was unlikely to have a significant impact on natural stabilisation-rejuvenation cycles in the greater dune system, native foredune communities were threatened by marram grass through habitat loss, competition and potential elimination via burial (Baye, 1990).

The invasion of marram grass into Australian dune systems has also had a substantial impact on native communities. Bell (1988) documented a change in dune morphology resulting from marram invasion at several locations along the Gippsland coast of Victoria where the low and wide foredunes characteristic of native grasses were replaced by hillocks as high as 5m. Marram grass was also introduced to New South Wales, with the expectation that it would die out after 7 – 12 years due to the predominant Australian conditions (Soil Conservation Service, 1990). However, there has been no subsequent decline in marram grass and there is significantly fewer native plant species on dunes stabilised with marram grass for 12 years compared to undisturbed dunes (Webb *et al.* 2000).

1.3.5 Marram grass in New Zealand

Marram grass was first recorded in New Zealand at Miramar Peninsula, Wellington in 1873 (Buchananan, 1873). Following introduction, marram grass has a history of facilitated spread from both government initiatives and agricultural practice. The main motivations for the planting of marram grass included the protection of infrastructure, dune afforestation and the stabilisation of mobile dunes (Gadgil and Ede, 1998). The inundation of farmland and valuable coastal property by sand was seen as a significant risk to the New Zealand economy and infrastructure. The planting of marram grass therefore aimed to convert dunes of marginal productive value into more ‘productive’ uses (Gadgil, 2006).

Despite its widespread planting, marram grass is a major threat to New Zealand’s coastal biodiversity and landform diversity. This is clearly portrayed in the decline of New Zealand’s active dune systems during the twentieth century (Hilton, 2006). In Cockayne’s (1911) survey of coastal dunes, he recorded a total area of 128,740ha. Hilton’s (2006) subsequent study documented the total coastal dune area between 1950 and 1990. In 1950, the coastal dune area was similar to that documented by Cockayne (1911); however by 1990, there was a reduction in total dune area to 38,949ha. This represented an approximate decline of 70% of the 1950 total area. Hilton (2006) listed the main causes for this loss as sand mining, stock grazing, infrastructure, urbanisation and the introduction of exotic plant, shrub and tree species. Hilton *et al.* (2005) investigated the impact of marram grass on a local scale at Mason Bay, where it showed a very rapid range expansion over a 40-year period. Originally introduced to Mason Bay in the 1930's, it had spread to approximately 1.4ha by 1958, 17.8ha in 1978 and 74.9ha in 1998, representing a 5,024% increase in total area (Figure 1.2). Coupled with this range expansion was a displacement of native species such as Pingao through loss of preferred foredune habitat and burial (Hilton *et al.*, 2005).

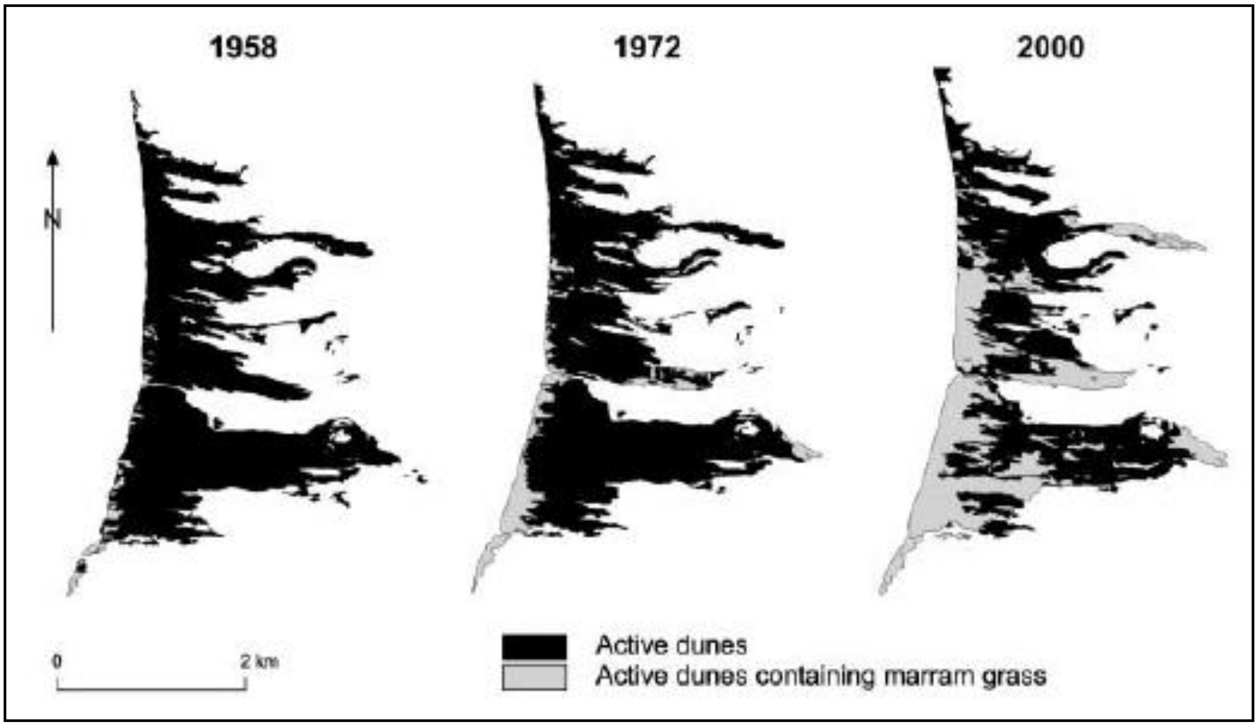

Figure 1.2: The extent of marram grass invasion in the central and northern dune systems of Mason Bay between 1958 and 1998 based on the interpretation of aerial photographs. *Source*: Hilton, 2006.

The sand trapping ability of marram grass' dense, tussock-like growth is credited with the formation of steep-sided hillocks that are often greater than sand's natural angle of repose (Huiskes, 1979; Summerfield, 1991). This changes the natural geomorphology of the dune environment where the indigenous sand-binding species produce small, hummocky dunes between 1-2m high (Esler, 1978). Stands of marram grass along the foredune can also facilitate the creation of a massive, continuous, prograding feature parallel to the coast (Figure 1.3) which is significantly different to the indigenous equivalent.

Figure 1.3: The massive, continuous marram grass foredune at Mason Bay.

Marram grass invasion is documented as a key cause for the decline of the native sand sedge Pingao, especially in South Island dune systems where there is little competition (Hilton *et al.*, 2005). On a local scale, it also threatens the critically endangered *Gunnera hamiltonii* colony at Mason Bay (Wilson and Given, 1989). Figure 1.4 highlights marram grass' dominance throughout New Zealand where it is the primary dune species along much of the coast around the lower North Island and most of the South Island. In Hilton *et al.*'s (2005) study of pingao displacement by marram grass at Mason Bay, it was concluded that pingao could not co-exist with marram and was threatened with local extinction where both species came into contact.

These findings were partly contradicted by Partridge (1995) who concluded that pingao and marram grass can co-exist in three situations; 1) on the front face of the foredune as a result of marram grass' reduced tolerance of salt concentration; 2) where moisture in the upper layers of the soil is not limiting; and 3) where both species are moribund in areas of limited sand supply. In all other cases however marram grass will displace pingao from the active dune system where they interact (Partridge, 1995). Despite the three anomalies in Partridge's (1995) findings, marram grass still represents a serious threat to New Zealand's coastal biodiversity.

The threat of marram grass to the natural values of New Zealand's coastal dunes lead to the initiation of the Stewart Island Marram Eradication Program (henceforth the MEP) in 1998, which is likely one of the largest marram grass control operations by area (Hilton and Konlechner, 2010). Its primary goal is to "restore and safeguard the geomorphic processes that underpin the natural character of the pre-marram dune-barrier system" (Hilton and Konlecher, 2010, pp. 387). It involves a partnership between the Department of Conservation (henceforth DOC) and the University of Otago that aims to carry out the eradication of marram grass with the support of research. This highlights the need to further understanding of the processes that drive dispersal and invasion such as seed ecology. Research from the MEP has indicated that sexual reproduction plays an important role in marram grass invasion and provides justification for the current research. The following sections will therefore introduce the key aspects of sexual reproduction in marram grass.

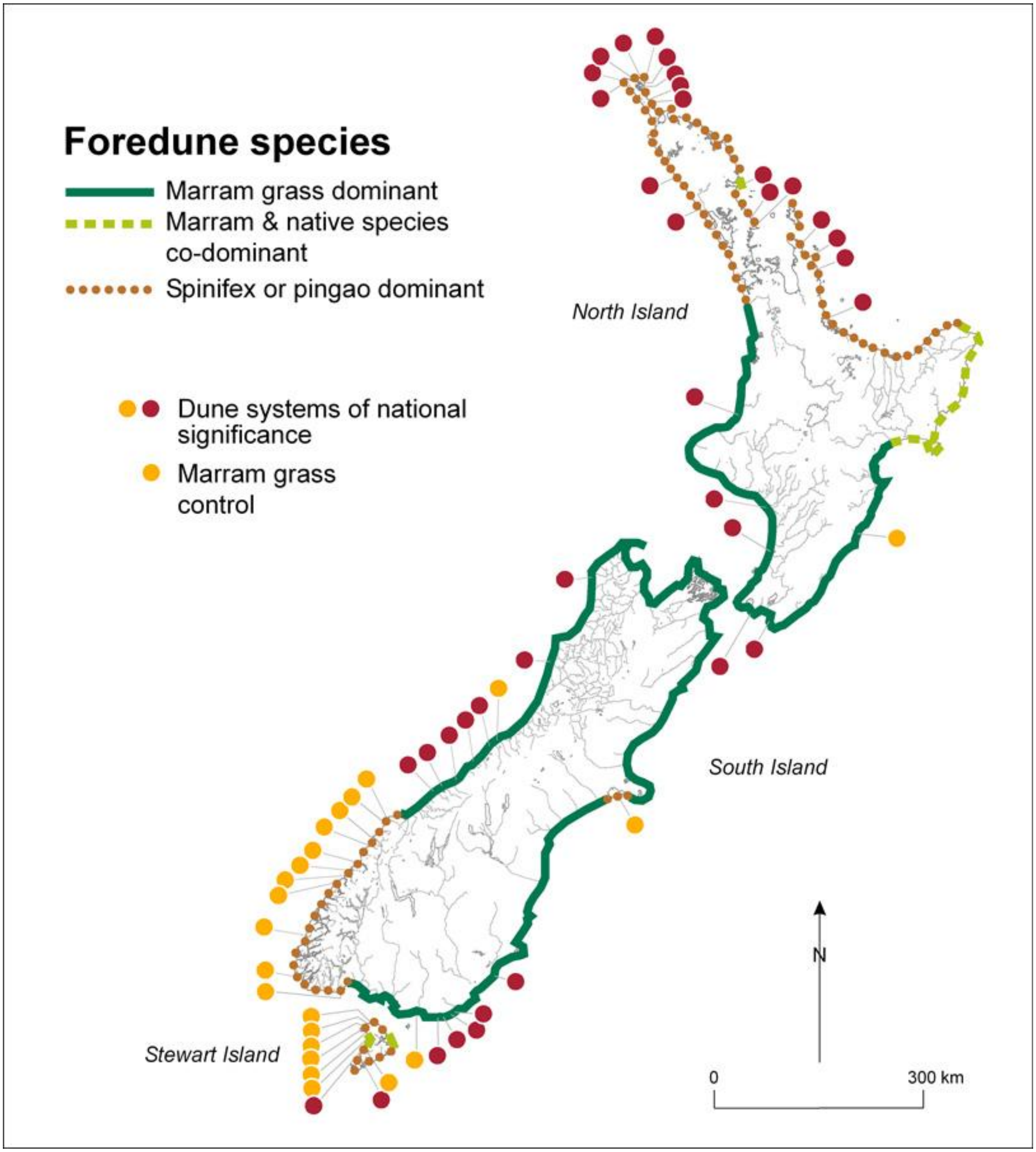

Figure 1.4: Marram grass distribution along coastal New Zealand and the location of nationally and/or internationally significant dune systems. *Source*: M. Hilton, Pers. Comm.

1.4 Sexual reproduction in marram grass

Very few studies in the available literature have focused solely on marram grass seed (e.g. Huiskes, 1977), as it has largely been regarded as being less important to the general ecology of marram grass (Huiskes, 1979; Hertling and Lubke, 1999; Krajnyk and Maun, 1982; Maun, 1984). It is important however to note that much of the literature relating to marram grass seed ecology is focused around European-based research, which is the natural range of marram grass and a region which has seen marram grass planted as a sand stabiliser from as early as the 14th century (van der Maard, 1981). Despite this, there have been some studies indicating the potential for marram grass seed to pose an invasive threat (e.g. Esler, 1974; Laing, 1958; Huiskes, 1977). Research conducted in association with the MEP also suggests that marram grass seed is capable of establishing in large numbers in the central dune system at Mason Bay (see Chapter 4) and that marram grass may possess a seed bank (Chapter 5) (Konlechner and Hilton, 2009).

This highlights key gaps in the understanding of the invasion process in marram grass and therefore this study will investigate five key aspects of seed ecology: 1) seed production; 2) dispersal; 3) dormancy; 4) germination; and 5) the seed bank. Seed production is discussed separately in Chapter 2 and dispersal is discussed in relation to the distribution of seedlings in Chapter 4, while the remaining aspects are reviewed below.

1.4.1 Dormancy and factors affecting dormancy

Burial can lead to the induction of dormancy in seed (Wesson and Wareing 1969a, b) which can be triggered by poor oxygen content, higher carbon dioxide levels, altered moisture content in the soil or the release of an inhibitor from the seed itself (Harper, 1977; Huang and Gutterman, 1998; Wesson and Wareing, 1969a). Dormancy can be broken by several factors often working in concert and that change with depth in the soil. These can include cold stratification of the seeds, the availability of oxygen and moisture, mechanical damage to the seed coat, release from chemical inhibitors and/or changing light regimes, photoperiods, spectral quality and intensity (Baker, 1989; Huang *et al.*, 2004; Wesson and Wareing, 1967, 1969b).

Dormancy was first classified by Nikolaeva (1977) into two broad types: 1) endogenous; and 2) exogenous. These were further categorised into physiological, morphological, morpho-physiological, physical, chemical and mechanical dormancy, which are summarised in Table 1.2. Marram grass seed is classified as possessing a physiological dormancy resulting from a physiological mechanism within the embryo that inhibits the emergence of the radicle (Baskin and Baskin, 1998). Nikolaeva (1977) distinguished three levels of physiological dormancy (henceforth PD). Non-deep PD is common in the seeds of most weedy species and usually includes those seeds that are unable to germinate at any given temperature or will germinate within a narrow range of temperatures. Breaking this form of PD may require cold stratification (although this is not essential), exposure to high temperatures or chemicals as well as light. The mechanisms behind this form of dormancy are unclear but may include 1) low permeability of covering structures to oxygen; 2) the prevention of leaching or oxidation of molecular inhibitors from embryos by these structures; 3) the mechanical restriction of embryo growth and/or 4) potential changes to the resistance of the endosperm, seed coats or other structures to penetration by the radicle (Nikolaeva, 1977). The second type, 'Intermediate PD', differs from non-deep PD because a period of cold stratification is necessary to break dormancy. 'Deep PD', like 'Intermediate PD' requires a period of cold stratification, although this needs to be much longer and is also the only treatment that overcomes dormancy.

Table 1.2: A summary of Nikolaeva's (1977) classification scheme for seed dormancy and the requirements for breaking this dormancy (from Baskin and Baskin, 1998).

Type	**Cause**	**Broken by**
Endogenous dormancy		
Physiological	Physiological inhibiting mechanism of germination	Warm and/or cold stratification
Morphological	Undeveloped embryo	Appropriate conditions for embryo growth
Morpho-physiological	A combination of both the above types of dormancy	Both of the above requirements
Exogenous dormancy		
Physical	Seed coats impermeable to water	Opening of specialised structure
Chemical	Germination inhibitors	Leaching of seed
Mechanical	Woody structures restrict growth	Warm and/or cold stratification

1.4.2 Seed germination

Maun (2009) identified three basic requirements for seed germination: 1) the availability of oxygen, 2) an appropriate temperature range; and 3) sufficient soil moisture. In empirical studies investigating the germination requirements of plant species, the primary factors affecting germination were temperature and soil moisture (Fulbright *et al.*, 1983; Gulzar and Khan, 2001). Optimal temperature ranges and soil moisture levels for germination often reflect spring growth conditions (Fulbright *et al.*, 1983). In the semi-desert grassland of the American Southwest, 60% to 70% of annual precipitation falls between July to October, which can make conditions mesic enough to facilitate germination (Winkel *et al.*, 1991).

In the coastal dune environment there is pronounced variability in factors promoting seed germination as a result of the constant shifting of substrate and other factors such as low levels of shading from plants, high soil porosity and virtually no organic matter (Huiskes, 1979; Maun, 2009; Zhang and Maun, 1994). Burial plays a key role in changing these microenvironmental conditions experienced by seeds. The effects of burial include the restriction of light penetration to buried seed (van der Meijden and van der Waals-Kooi, 1979), increased activity of mycorrhizal fungi and increased soil resources (Maun, 1998). This study therefore aims to investigate two key factors related to germination in coastal dune systems, the effect of light and darkness on seed germination and the ability of seedlings to emerge from burial, in order to better understand those processes affecting the germination of buried marram grass seed (Chapter 3).

1.4.3 The seed bank

The seed bank is defined as an aggregation of all un-germinated, viable seed on or in the soil and/or contained within the associated plant litter, which is potentially capable of replacing adult plants (Baker, 1989; Simpson *et al.*, 1989). Additions to seed banks can come from the dispersal of fresh seed from local sources or immigration from more distant fruiting populations, whilst outputs can include germination (premature or successful), predation, senescence, disease and fungal attack (Baskin and Baskin, 1998; Maun, 2009; Simpson *et al.*, 1989). It is the balance between these processes that determines the abundance of a species' seed bank.

Many authors state that there is a correlation between the increasing persistence of seed banks and seed size, with greater longevity shown in seeds of a smaller size (Baskin and Baskin, 1998; Peco *et al.*, 2003; Thompson, 1987). Thompson (1987) also noted that seeds of grasses that possess persistent seed banks are often small and compact, with structures such as awns aiding successful burial by actively pushing the seeds into surface cracks or passively influencing the orientation of seeds.

The longevity of seed banks is highly variable, with some species possessing no seed bank at all, while others may possess either a transient or persistent seed bank (Simpson *et al.* 1989). Transient and persistent seed banks can be classified into four categories: Type I) a transient seed bank present during summer; Type II) a transient seed bank present during winter; Type III) a persistent seed bank with a large proportion of seeds germinating following dispersal and only a small percentage buried; and Type IV) a persistent seed bank with few seeds germinating before incorporation into the soil (Thompson and Grime, 1979). Thompson *et al.* (1998) further categorised longevity into four types: Type I) a transient seed bank persisting for less than 1 year; Type 2) a short-term persistent seed bank persisting for greater than 1 year but less than 5 years; Type 3) a long-term persistent seed bank persisting for greater than 4 years; and Type 4) for those species that cannot be assigned to any of the previous three.

1.5 Research objectives and questions

The paucity of literature relating to sexual reproduction in marram grass is largely a result of the perception that seed plays a less important role in the invasion ecology of marram grass. In southern New Zealand however, observational evidence from the MEP suggests that invasion via seed may play a much more important role in marram grass invasion than was previously thought.

This study therefore aims to determine the potential for marram grass re-invasion from secondary seed dispersal and *in situ* germination. To achieve this aim, two objectives were identified with three key research questions contained in each:

1) To investigate the role of secondary seed dispersal in marram grass invasion in transgressive dune systems.
    a. Does downwind seed transport contribute to marram grass invasion in transgressive dune systems in southern New Zealand? How far are seeds transported?
    b. Which environments favour (i) germination and (ii) emergence?
    c. Which factors affect germination and emergence in different depositional settings?
2) To determine if marram grass forms viable seed banks in southern New Zealand.
    a. Does marram grass form viable seed banks in southern New Zealand?
    b. How long does seed remain viable?
    c. What proportion of seed remains viable?

1.6 Field Sites

Field work was carried out at four dune systems around southern New Zealand (Figure 1.5). Mason Bay, on the west coast of Stewart Island, was used as a case study for the estimation of marram grass seed crop size in southern New Zealand (Chapter 2). The extensive transgressive dune system and large flowering marram population at Mason Bay also provided an ideal site for the analysis of seedling distribution in dune systems (Chapter 4). The flowering population of marram grass at Oreti Beach was used as a source of seed for the germination experiments (Chapter 3). Allan’s Beach and St Kilda Beach, located on the Otago coastline, provided a unique opportunity to sample and age the marram grass seed bank (Chapter 5).

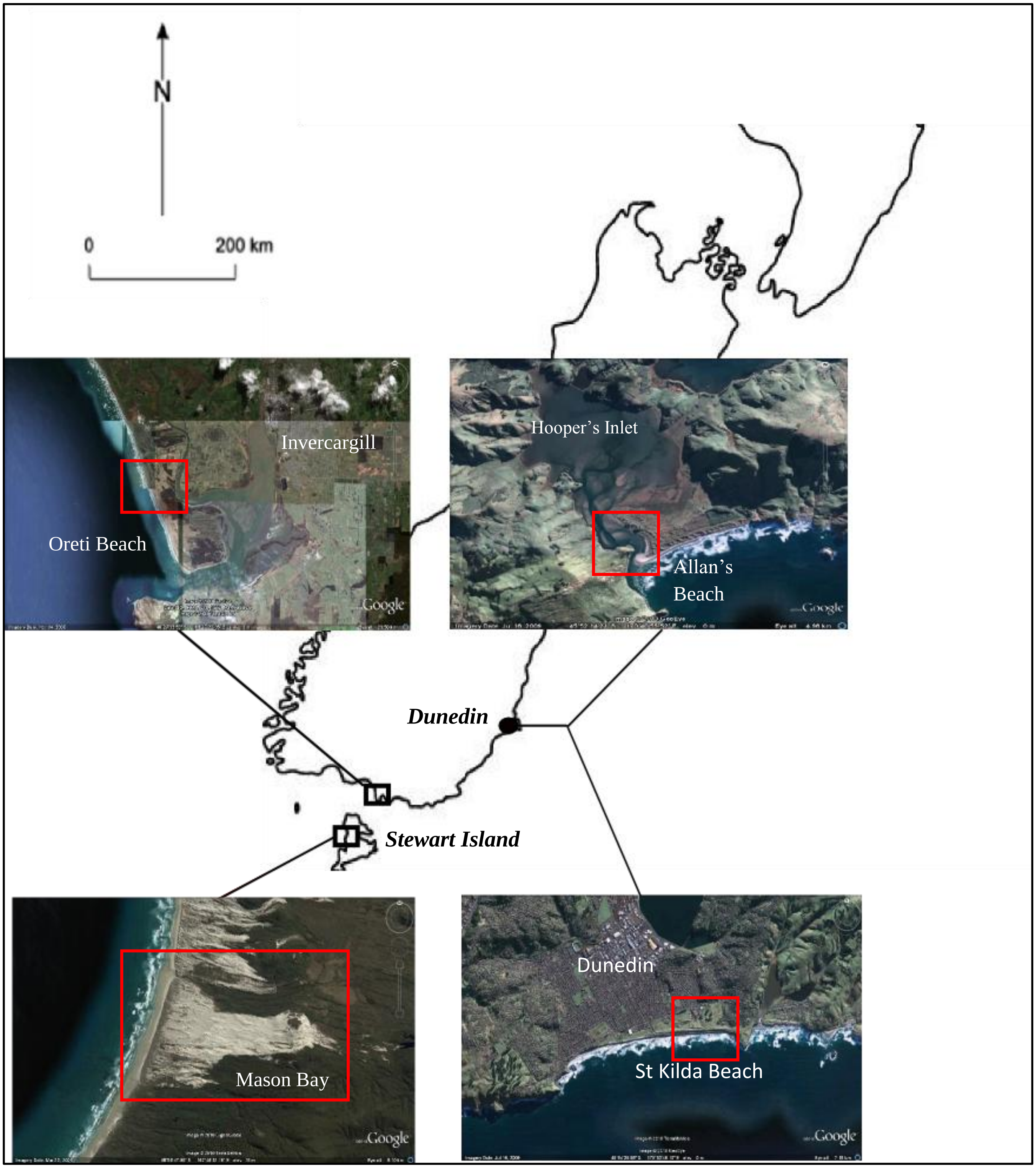

Figure 1.5: A map showing the four study sites in southern New Zealand (from the top left and moving clockwise), Oreti Beach, Allan's Beach, St Kilda Beach and Mason Bay. Each inset has the study site marked as a red square.

1.7 Thesis structure

Chapter 1 has provided an overview of the context for the study through a general literature review. Invasive weeds are those plant species that are able to spread naturally into habitats and produce a significant change to biodiversity and ecosystem function. Marram grass is one such successful invader globally and in New Zealand. Literature states that its predominant mode of invasion is vegetative however evidence from southern New Zealand suggests that sexual reproduction plays a more important role than previously thought. This study therefore investigates key aspects of marram grass seed ecology in order to further understanding of this phenomenon.

Chapter 2 estimates marram grass seed crop size in six depositional environments at Mason Bay. A brief review of literature relating to previous estimates of seed crop size in marram grass is conducted as well as an introduction to those factors affecting vigour. The quantification of flowering density m^{-2} and the number of florets per flower spike were used to estimate seed crop size. Differences in estimated seed crop size between the depositional environments are discussed in relation to those factors affecting marram grass vigour.

Chapter 3 investigates two key factors in the germination of marram grass seed; the effects of light and darkness and the impact of burial. The germinability and viability of marram grass seed in southern New Zealand is also investigated. This chapter aims to determine the relationship between light, darkness and burial with respect to marram grass seed germination.

Chapter 4 analyses seedling distribution patterns in data gathered from Mason Bay. This develops an understanding of those microsites that provide ideal conditions for the germination of marram grass seed. The potential mechanisms behind seedling distribution are discussed and this information is used to inform the development of a conceptual model of invasion.

Chapter 5 investigates the nature and longevity of the marram grass seed bank. Two unique methods of sampling the seed bank are described from two study sites. The results from longevity and viability investigations are then presented. These findings are discussed with respect to the potential for marram grass seed bank formation in southern New Zealand.

Chapter 6 synthesises the findings of objective one into a conceptual model of invasion. The assumptions inherent in the development of the model and future research directions are also discussed.

Chapter 7 summarises the main findings and conclusions of the study. These also form the basis for the management recommendations for future marram grass eradication operations which are a key outcome of the study.

Chapter 2

Seed production at Mason Bay, Stewart Island

2.1 Overview

The dispersal of seeds into the dune hinterland forms a ‘rain’ of seeds which have one of three fates: 1) they may become dormant and survive in the substrate; 2) they may germinate into seedlings and establish or die from a variety of causes i.e. desiccation; or 3) they may be transported elsewhere via secondary dispersal (Rabinowitz and Rapp, 1980). The dune environment presents particularly harsh conditions for seeds to germinate and establish in (Maun, 2009), however the production of many seeds may increase the chance that at least a few individuals will disperse to sites ideal for establishment (Willson, 1993). Objective one of the study aims to investigate the role of secondary dispersal of seed in marram grass invasion in transgressive dune systems. This chapter therefore aims to investigate a key aspect of marram grass seed ecology, the production of seed in flowering marram grass populations of southern New Zealand. By estimating seed crop size, this study hopes to assess the potential invasive threat that marram grass poses via seed dispersal.

2.1.1 Propagule pressure

Propagule pressure can be defined as the rate at which propagules and seeds are released into a new environment (Williamson and Fitter, 1996). Along with rate of disturbance, increasing propagule supply is found to increase the success of invasion at specific sites (Crawley *et al.*, 1999; Kellogg and Bridgham, 2004). Levine *et al.* (2003), in their review of 150 studies investigating the mechanisms underlying the impacts of exotic plant invasions, concluded that given sufficient propagule supply (or propagule pressure), few communities are likely to remain free from invasion. During the early stages of invasion, the spread of a plant species is largely constrained by propagule supply rather than habitat availability (Rouget and Richardson, 2003). Once an invader has established in a new site however, seed production from within the habitat quickly overwhelms the influx of propagules from outside the environment and greatly exceeds the seed supply prior to initial colonisation. D'Antonio *et al.* (2001) also note that where environmental resistance (abiotic or biotic) is strong; propagule supply must be large to overcome any barriers to establishment. In coastal environments, while biotic resistance is generally low, abiotic resistance is high because of factors such as desiccation and burial (Maun, 2009). Therefore, coastal dune environments, an invasive species would require a large propagule supply in order to successfully establish.

At Mason Bay, initial propagule pressure originated from the planting of marram grass by farmers at Kilbride in the 1930's (Hilton *et al.*, 2005) (Figure 2.1) and from dispersal of rhizome via ocean currents (Konlechner, 2008). Marram grass at Mason Bay gradually spread over a 60 – 70 year period, forming the massive flowering foredune complex that exists today. This represents a significant source of seeds from which invasion into the dune hinterland can proceed. In an environment such as Mason Bay, small populations are likely to succumb to stochastic (environmental variation) effects. Therefore the repeated release of large numbers of propagules into a location helps to sustain invasion by marram grass (Lockwood *et al.*, 2005). As well as the foredune complex, several other depositional environments within Mason Bay contain populations of flowering marram grass with differing vigour. Estimating seed crop size in each of these environments is of particular importance because it furthers understanding of the potential for marram grass to invade via seed.

2.1.2 Estimates of seed crop size in marram grass

Few empirical studies of reproductive output in marram grass exist, making it difficult to estimate the potential for marram grass to invade via seed into dune systems. In two studies by Salisbury

(1942, 1952) estimates of seed production per clump of flower spikes were 35,650 and 20,000 respectively. These figures are in stark contrast to the findings of a study conducted by Laing (1958) in *Ammophila breviligulata* which estimated seed crop size to be 846 seeds m^{-2}. Krajnyk and Maun (1982) in another study of reproductive output in *A. breviligulata* identified a flowering density of 0 – 8.5 individuals m^{-2}, with the number of seeds per flower spike ranging between 141 - 232 across two separate years and sites. Combined, these figures suggest an estimated maximum seed crop size of 1,972 seeds m^{-2}. The significant variation between the estimates of the four empirical studies highlight a key gap in the knowledge of reproductive output of marram grass, which this study hopes to investigate.

2.1.3 Marram grass vigour

Estimation of seed crop size between each of the depositional environments will vary depending on the vigour of the flowering marram grass populations, which are affected by differences in wind regimes and sand supply among other factors (Disraeli, 1984; Eldred and Maun, 1982). As described in Chapter 1, as marram grass forms a more stable dune environment it loses vigour, in a phenomenon termed the ‘Ammophila problem’ (Marshall, 1965). It would therefore be expected that marram grass will be less vigorous in those depositional environments that are relatively stable and receive lesser volumes of aerially transported sand.

Eldred and Maun (1982) in a study of the decline in vigour of *A. breviligulata* showed that sand accretion had the greatest influence on vigour. They advanced the following successional hypotheses: 1) in young dunes with sand accretion, *A. breviligulata* is vigorous but shoot density is sparse, resulting in a greater loss of sand and the establishment of a greater number of annual species; both of which reduce flowering levels. 2) As sand deposition continues, population size increases, excluding annuals and allowing for prolific flowering and shoot development. This environment contains populations of *A. breviligulata* with the greatest vigour. 3) Once the dunes begin to stabilise, sand deposition decreases, resulting in the decline of shoot vigour and flower spike production, with a corresponding increase in vegetative reproduction. 4) Finally in the latter stages of stabilisation, changes in other variables and the reduction of sand movement probably allows for the invasion of other species which are able to out-compete *A. breviligulata* for resources. This is evidenced by the greater depth of adventitious roots in *A. breviligulata* in the presence of annuals, suggesting competition for water and nutrients.

Disraeli (1984) also found increased vigour in *A. breviligulata* with increasing sand deposition. In Disraeli's (1984) investigation of changes in morphology, biomass, total chlorophyll concentration and nitrogen fixation, it was found that depth of yearly sand burial had a positive effect on all factors except horizontal rhizome growth. This strongly suggests that *A. breviligulata* vigour increases with increasing rates of sand accretion. Although the effect of sand deposition on flowering was not investigated by Disraeli (1984), it could be expected that increases in the vigour of an *A. breviligulata* individual could have corresponding increases in seed crop size due to a greater availability of resources.

2.2 Method

2.2.1 Introduction

In order to estimate the reproductive output of marram grass at Mason Bay, three aspects of the flowering population were investigated during January 2010 and May 2010. These included the flowering density m^{-2}, the average number of florets per flower spike and the estimation of seed crop size in six different depositional environments of Mason Bay. The following section begins with a description of the study site followed by the method used to investigate these aspects of reproductive output.

2.2.2 Study site – Mason Bay, Stewart Island

Mason Bay is one of the largest and most significant west coast transgressive dune systems in New Zealand. It is considered important on both a national and international scale due to its biodiversity and landform diversity (King and Hare, 1990; Patrick *et al.*, 1990). The area is considered outstanding not only because of its size but also for its diverse landforms, habitats, richness of dune flora and large tracts of unmodified active dunes; all of which are under threat from the spread of marram grass (Johnson, 1982).

Mason Bay (Figure 2.1) is approximately 13km long and is backed by dune systems that are between 1.2km and 3.5km wide (Hilton, 2006; King and Hare, 1990). A combination of available sediment and prevailing onshore westerly winds has resulted in the development of the extensive transgressive dune system (Hilton *et al.*, 2005). Mason Bay encompasses a wide range of communities including the foredune vegetation in the west, a broadleaf forest separating the northern and central dune systems, the central dunefields which contain long-walled parabolic dunes and stonefields and a mature podocarp forest along the southern boundary (Hilton, 2006).

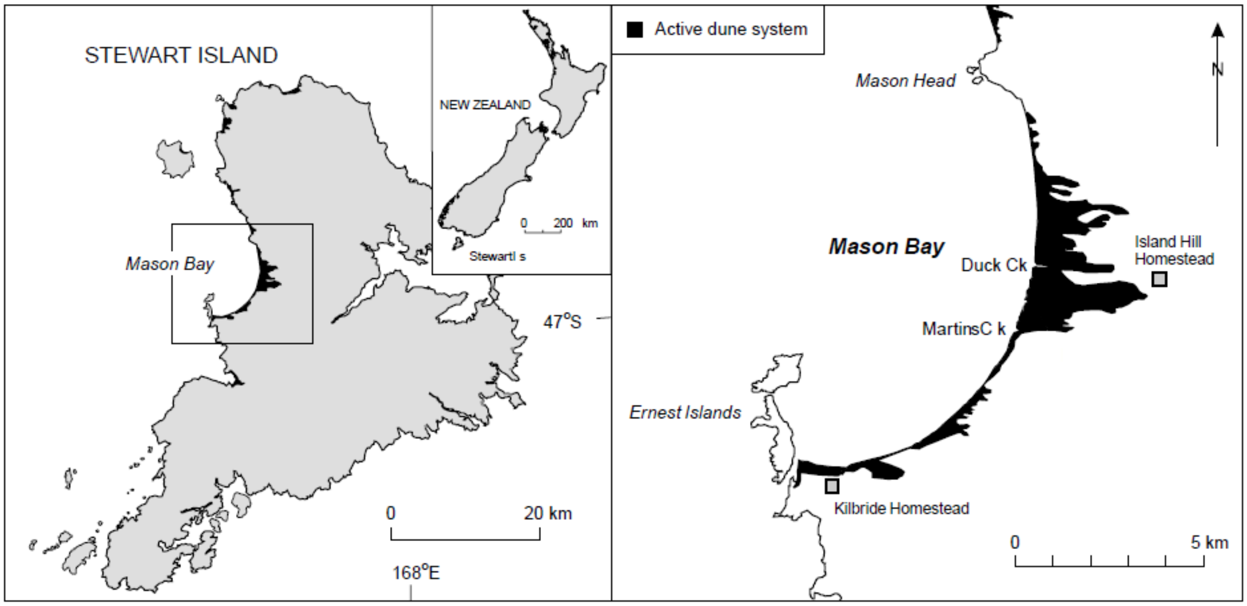

Figure 2.1: The location of Mason Bay, Stewart Island, New Zealand. *Source*: Hilton et al., 2005.

Following planting, the rapid spread of marram grass represents a serious threat to Mason Bay's native communities. Patrick *et al.* (1990) recorded up to 94 dune plant species at Mason Bay, with the significance of several species summarised in Table 2.1. Tall, rank species such as marram grass have also been documented to provide cover for predators, which could negatively impact on Mason Bay's avifauna such as the Stewart Island Kiwi (*Apteryx australis*), and reduce breeding areas of shorebirds such as the Variable Oystercatcher (*Haematopus unicolor*) and New Zealand Dotterel (*Charadrius abscurus*) (King and Hare, 1990; Moore and Davis, 2004). The threat that marram grass poses to Mason Bay's internationally and nationally significant communities therefore drives the investigation of the marram grass invasion process at this study site.

Table 2.1: Selected examples of rare or nationally significant plants within Mason Bay. *Source*: King and Hare (1990); Patrick et al. (1990).

Species name	Significance of plant species
Gunnera hamiltonii	A critically endangered species with only a few sites on the west coast of Stewart Island and one site on the Invercargill coast. This species requires active management in order to survive.
Euphorbia glauca	Only four sites on Stewart Island, all at Mason Bay.
Luzula cellata	Rare nationally and only known on Stewart Island from the landward sand blows of Big Sandhill and Sandhill Pass.
Ficinia spiralis	Still common but decreasing through competition with marram grass nationwide (formerly *Desmoschoenus spiralis*, Pikao/Pingao).

2.2.3 Marram grass flower spike collection

Flower spikes were gathered from Mason Bay during May 2010. By May, the seeding period had already ceased for the marram population, however, unfortunately due to time and money constraints this was the earliest opportunity to gather flower spikes. Although the author was present at Mason Bay in January 2010 (section 2.2.4), seed development was deemed to be immature, preventing the collection of flower spikes for the quantification of florets per flower spike during the summer of 2009/2010. A total of 120 flower spikes were collected from six depositional environments including the Foredune Complex, the Northern Dune System Nabkha, the Trailing Arms and Coppice Dunes of the parabolic dunes and the Nabkha and Sandsheets of the Backdune region at Mason Bay (see Figure 2.2). These were chosen to represent flowering marram grass populations in depositional environments with varying levels of disturbance and fresh sand supply which is important in the production of seed by marram grass.

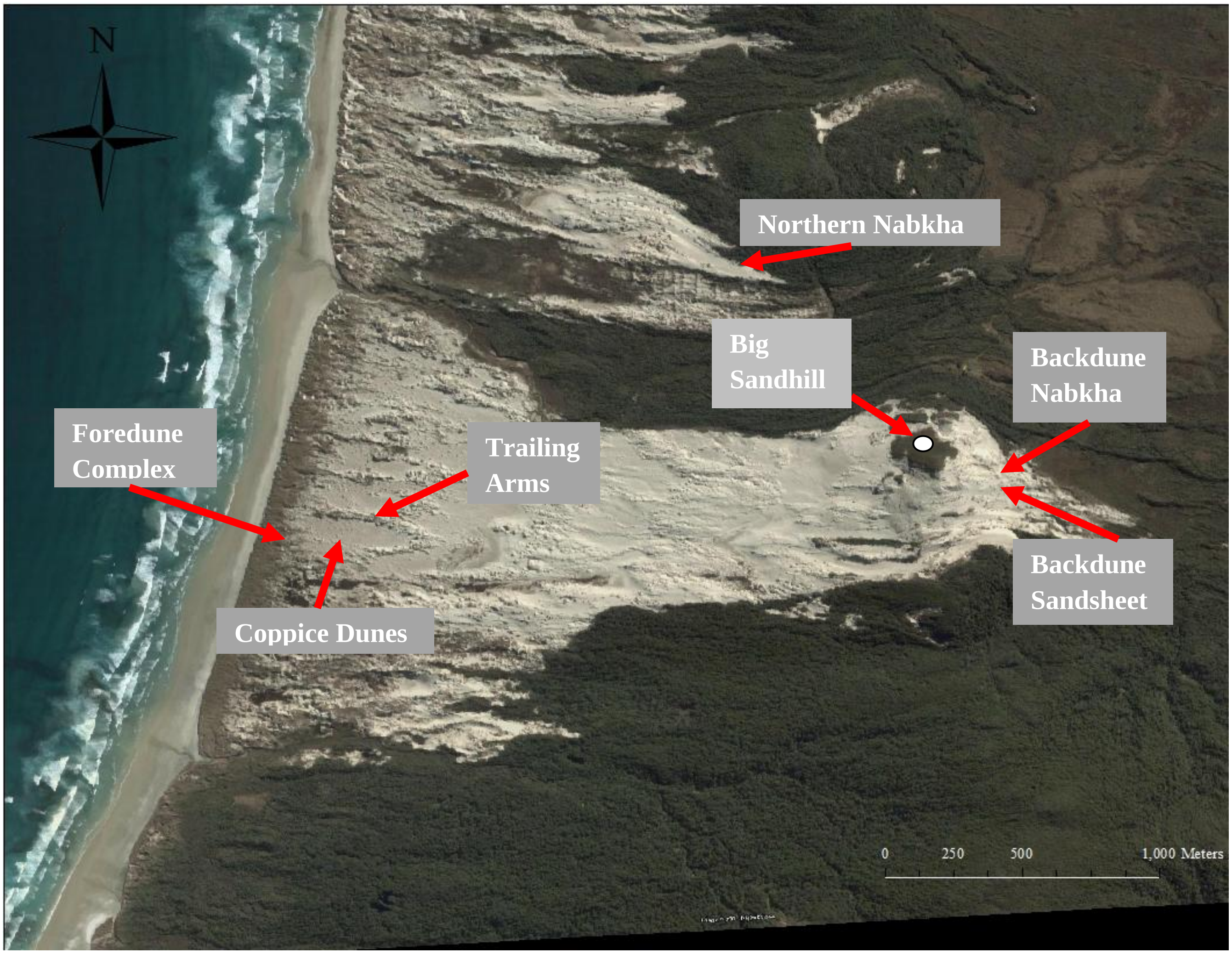

Figure 2.2: A map of the northern (partial) and central dune systems at Mason Bay and the six sampled depositional environments. The landmark ‘Big Sandhill’ is also marked for future reference.

2.2.3.1 The foredune complex

The foredune complex (Figure 2.3) consists of a massive 10 - 15m high foredune, orientated parallel to the coast and extending between 80 - 100 metres from the dune face to its most landward extent. For this study, the complex was separated into the Foredune Face, which extends from the base of the foredune to the peak, the Foredune Mid-zone which included the plateau-like central part of the complex and the Backdune Face which begins at the point where the foredune slopes down towards a deflation surface (Figure 2.4). In a slight deviation from the florets per flower spike sampling method used in the other depositional environments, 15 flower spike samples were collected from each of these sub-sections in order to improve statistical tests conducted on seed production within the foredune complex.

Figure 2.3: A set of photographs depicting the foredune complex at Mason Bay. (Top Left) The foredune face; (Top Right) a view from the top of the foredune overlooking the foredune face; (Bottom Left) the plateau of the foredune mid-zone; and (Bottom Right) the backdune region of the foredune complex. *Photo*: Teresa Konlechner.

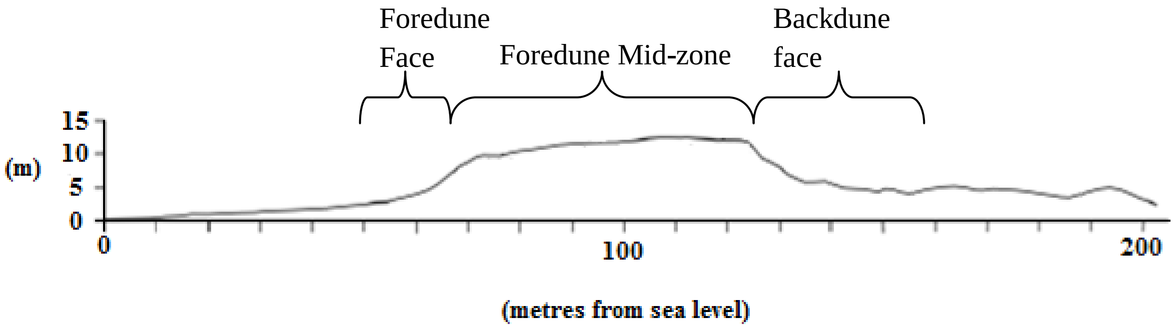

Figure 2.4: A profile of the foredune complex of Mason Bay with the three units marked. *Source*: Petersen (2010).

2.2.3.2 Northern nabkha

The northern nabkha depositional environment refers to a series of nabkha dunes in the northern dune system of Mason Bay (Figure 2.5). These nabkha dunes range from 0.3m to 2.3m high and have dense, healthy, flowering stands of marram grass. This area is exposed to strong westerly winds, which is often reflected in the long tail of the nabkha in this depositional environment.

Figure 2.5: The northern nabkha are a set of exposed nabkha dunes in the northern dune system of Mason Bay. Photo: Jean Wilson.

2.2.3.3 Trailing arms and coppice dunes

The flower spikes of the marram grass population on the trailing arms were collected from the long-walled parabolic arms adjacent to the foredune complex (Figure 2.2). These are relatively large, stable, vegetated depositional features 5 - 10m tall which terminate in a depositional face approximately 200m from the end of the foredune complex. The marram grass population on the trailing arms appeared to be moribund compared with those populations in more exposed and dynamic depositional environments, characterised by higher rates of sedimentation (Figure 2.11). The coppice dune population of marram grass was contained on the deflation surfaces between these trailing arms (Figure 2.2). These consisted of low, hummocky dunes approximately 0.5m to 2m high with scattered flowering contained on the coppice dunes. Due to the nature of the deflation surfaces (i.e. generally erosional), large amounts of sand accumulation were not observed despite wind-blown sand being regularly transported through this dune environment.

2.2.3.4 Backdune nabkha and sandsheets

The backdune region of Mason Bay is located on the eastern side of Big Sandhill (Figure 2.2) approximately 2.5km from the coast and consists of a series of nabkha dunes and sandsheets. On the nabkha, marram grass appeared to be very healthy with vigorous, dense flowering, similar to that observed in the northern nabkha marram grass population (Figure 2.6). The marram grass population on the sandsheets also showed relatively vigorous flowering although this was scattered over a much greater area compared to the nabkha and was not as dense.

Figure 2.6: One of the exposed backdune nabkha east of Big Sandhill showing vigorous flowering.

2.2.4 Density of flowering in depositional environments

An investigation into the density of flowering m^{-2} in each of the depositional environments was carried out in January 2010. Sampling methods varied between depositional environments depending on the area to be sampled and are explained in detail below. Table 2.2 summarises these variations in sampling strategy.

2.2.4.1 The foredune complex

The foredune complex was sampled using three transect lines spanning the foredune complex. Within these transect lines; the foredune complex was divided into three sections, the foredune face, the foredune mid-zone and the backdune face (Figure 2.4). The foredune mid-zone was further sub-divided into three 10m sections to enable a greater spread of quadrat sampling in this section. Once a transect line had been established, a grid 10m (foredune mid-zone) or 12m (foredune face and backdune face) long and 12m wide was created. This setup enabled the random placement of 30 0.5 x 0.5m quadrats along each of the three transect lines. The number of flower spikes that fell within the quadrat was also counted and 15 from each section were randomly cut and bagged for the investigation in section 2.2.5.

2.2.4.2 Northern nabkha

As nabkha are discrete and spatially scattered features, flowering density in this depositional environment was sampled through the selection of 19 nabkha of varying sizes ranging from an area of 0.3 m^2 to 26.24 m^2 and 0.3 m to 2.3 m high (a list of all the sampled nabkha is provided in Appendix A). The dimensions (width, length and height) of each of the selected nabkha were measured as well as the height of the marram grass from upper surface of the nabkha to the tips of the grass blades. All flower spikes growing on the nabkha were then pulled and counted to avoid doubling up counts.

2.2.4.3 Trailing arms

Five trailing arms were sampled using 100 pace transects along the ridge of each arm. Quadrats were located using a random system which decided how many paces along the ridgeline transect each quadrat would be located and how many paces to the left or right from the ridgeline these would be placed. This was used in order to potentially sample the whole trailing arm from the base to the ridgeline. The quadrats were 1m x 1m in area and within each quadrat all the flower spikes were counted and a sub-sample was collected for the determination of estimated seed crop size in this depositional environment.

2.2.4.4 Coppice dunes

Sampling of the coppice dunes involved the placement of three transect lines perpendicular to the coast which were 200 m, 152 m and 160 m long respectively. These distances were dictated by the need to avoid overlapping of sampled coppice dunes and the dimensions of the sampled deflation surface. Previously to this study, the marram grass population in this deflation surface had been sprayed to a clearly visible line in 2008, which also affected the length of the transect lines.

All of the coppice dunes that fell directly under the measuring tape were sampled and a tally was taken of the number of non-flowering versus flowering coppice dunes. If marram grass on a coppice dune was flowering it had its dimensions measured (i.e. length, width and height) and flower spikes counted. Flower spikes were also cut once they had been counted to avoid counting the same head twice and to indicate where the previous transect lines had passed through as there was not enough equipment to leave in position. Three rules were also employed when sampling the coppice dunes: 1) only those coppice dunes with a 30+ cm dimension in any direction were included; 2) only those coppice dunes with marram grass on them were marked and measured; and 3) dimensions were measured from the widest and longest points of the coppice dunes. The area of the coppice dunes was subsequently calculated using the formula for a rhombus.

2.2.4.5 Backdune nabkha

In the backdune region of Mason Bay, all 11 of the local nabkha were sampled. Unlike the northern nabkha however, these nabkha were sampled with three to five 1m x 1m quadrats depending on their size. Sampling locations for these nabkha were decided by throwing a marker blindly in a random direction in an effort to reduce the time that would have been lost if a more systematic grid had been set up. Within each quadrat all flower spikes were counted and bagged for the florets per flower spike investigation (section 2.2.5).

2.2.4.6 Backdune sandsheets

The term ‘sandsheet’ in this study is used to describe the areas of sand colonised in marram grass that are not part of a nabkha feature. The sandsheet was sampled using two 100 pace transects which attempted to incorporate as much of the microtopography as possible (i.e. ridges and dune faces). Along each transect, 15 0.5m x 0.5m quadrats were randomly located to the right or left of the transect line using a similar random system to the trailing arms method. At each location all the flower spikes were counted and 15 were collected for the florets per flower spike investigation in this depositional environment.

Table 2.2: A summary of the different methods used in estimating the density of flowering in different depositional environments at Mason Bay.

	Depositional environment					
Sampling method	**Foredune complex**	**Northern nabkha**	**Trailing arms**	**Coppice dunes**	**Backdune nabkha**	**Backdune sandsheets**
# Transects	3	N/A	5	3	N/A	2
# Quadrats	90	N/A	75	N/A	51	35
# Whole features	N/A	19	N/A	N/A	N/A	N/A

2.2.5 Florets per flower spike

In order to determine the maximum number of seeds potentially produced by marram grass, 15 flower spikes per depositional environment were dismantled and the florets were counted (Figure 2.7). As mentioned previously, 15 flower spikes from each of the foredune complex units were sampled in a slight deviation to the method used in the other depositional environments. The number of florets per flower spike was averaged to gain some comparison across the depositional environments. The counts obtained during this exercise are considered to provide an estimate of ‘maximum potential seed set’ because seed production could not be ascertained by counting florets alone. Due to the collection of flower spikes after seed fall, individual caryopses were no longer present on the sampled flower spikes. Because each marram grass floret can only produce one seed, and the morphology of the spikelets, with a remnant pair of widely spaced sterile glumes, clearly indicates a seed was present in the majority of florets seen, using the number of florets per flower spike to estimate maximum seed production is a valid approach.

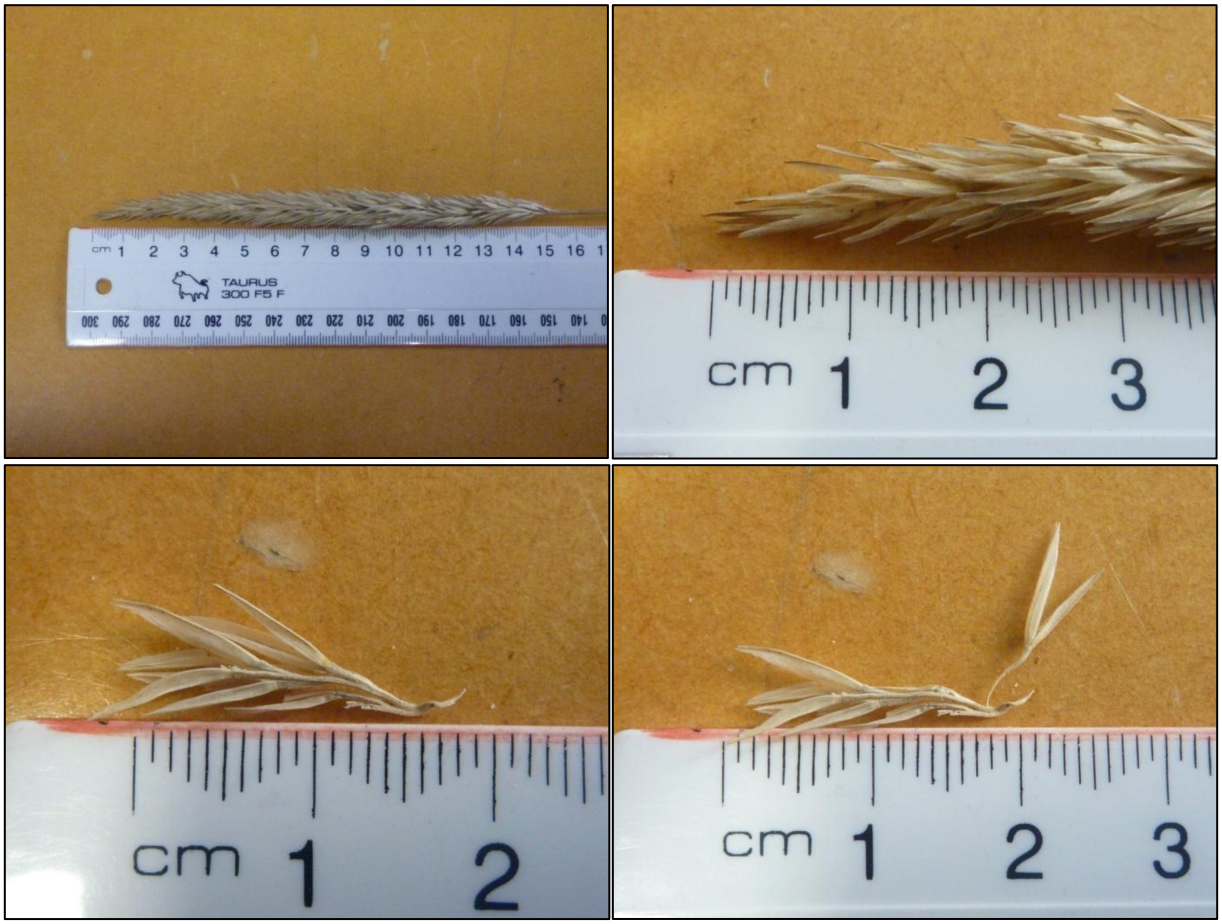

Figure 2.7: The floret counting process. (Top Left): A full flower spike is selected. (Top Right): A close-up view of the sampled flower spike. (Bottom Left): A section removed from the stalk to enable easier counting. (Bottom Right): Each bract is removed to avoid doubling up on counts.

Although counting florets is not the most accurate method for estimating seed production, it does provide an idea of the difference in relative crop size between depositional environments if it is assumed that florets in each depositional environment are equally likely to set viable seed. Counting seeds may also have been inaccurate as often seed caryopses form but they remain empty for reasons such as inadequate resource allocation due to adverse seed production conditions during seed development (Pope, 2005) gamete inviability (Church, 1929) and/or insect attack (Waterman, 1928).

2.2.6 Statistical analysis

Firstly, the density of flower spikes m^{-2} was calculated for each of the depositional environments. This was achieved by comparing the number of flower spikes counted against the total sampled area. This provided a value upon which a direct comparison could be made between all of the environments. A Kruskal-Wallis test using Minitab 15 provided a statistical measure of the difference between the foredune face, foredune mid-zone and backdune face of the foredune complex in order to elucidate any trends in reproductive effort that may arise through variations along this large depositional feature. In order to compare the differences in reproductive effort across all the depositional environments, a one-way ANOVA and Tukey's test were used because the variances of the data were deemed to be suitable for a parametric test (Bartlett's value, 0.062). To test the statistical difference between the three different sub-sections of the foredune complex however, a Kruskal-Wallis test was required.

2.2.7 Estimating maximum seed crop size in marram grass

The key outcome of this aspect of the study was to give an indication of the seed crop size of marram grass populations in southern New Zealand, which can be used as a comparison against the findings of other studies. The maximum potential seed crop size for each depositional environment was calculated by multiplying the density of flowering m^{-2} by florets per flower spike in a process similar to Laing's (1958). This produced a maximum potential seed crop size m^{-2} for each of the depositional environments which could later be compared against one another.

2.3 Results

2.3.1 Density of flowering in depositional environments

Flowering density varied greatly between the six depositional environments at Mason Bay (Table 2.3). The greatest densities were seen in both the northern and backdune nabkha (76.44 and 67.14 flower spikes m^{-2} respectively), whilst the lowest densities were seen in the coppice dunes and trailing arms (0.23 and 1.45 flower spikes m^{-2} respectively). Flowering density decreased with distance from the foredune face across the foredune complex, with flowering densities of 27.87, 10.67 and 1.6 flower spikes m^{-2} in the foredune face, mid-zone and backdune face respectively. The backdune sandsheets showed a density similar to that of the foredune mid-zone. The total area sampled from each of the depositional environments ranged from 517.9 m^{2} in the coppice dunes to 22.5 m^{2} in the foredune complex.

Table 2.3: A summary of the total area sampled, total number of flower spikes observed and density of flower spikes m^{-2} in each of the six depositional environments at Mason Bay.

Depositional environment	**Total area sampled (m^{2})**	**Total number of flower spikes**	**Density of flower spikes (m^{-2})**
Foredune complex	22.5	301	13.38
Foredune face	7.5	209	27.87
Foredune mid-zone	7.5	80	10.67
Backdune face	7.5	12	1.6
Coppice dunes	517.9	121	0.23
Northern nabkha	119.15	9,108	76.44
Backdune nabkha	51	3,424	67.14
Backdune sandsheets	30	274	9.13
Trailing arms	75	109	1.45

The separate units of the foredune complex were tested statistically to elucidate any trends across the depositional feature (Figure 2.8 and Table 2.4). There is a difference between the averages of each of the units of the foredune complex, with the foredune face having the highest mean followed by the foredune mid-zone and backdune face respectively. The outliers of the foredune face are also greater than those of the foredune mid-zone. The interquartile ranges for each of the foredune units also decreased with increasing distance from the foredune face.

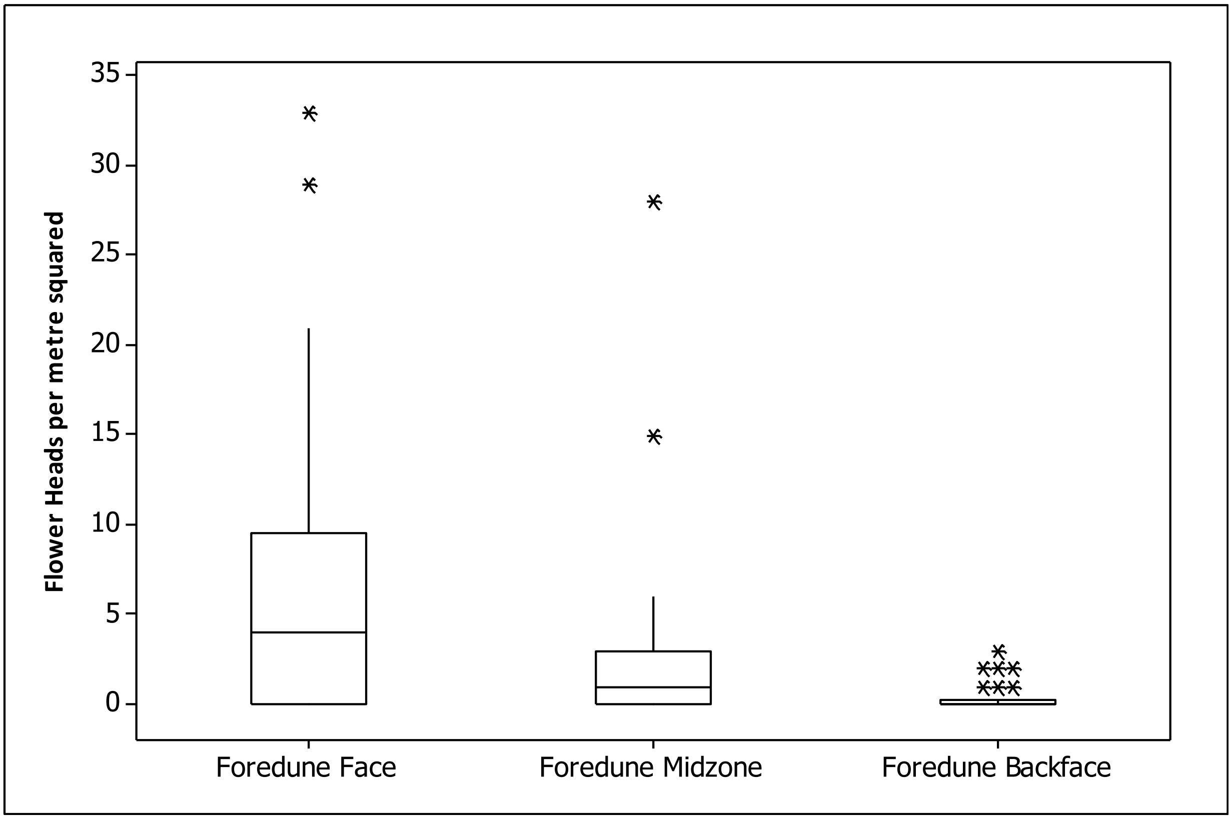

Figure 2.8: A comparison of density of flower spikes m^{-2} between the units of the foredune complex. For each box and whisker plot, the central line represents the mean number of seeds per spike and is bounded by the upper and lower quartiles. The stars represent suspected outliers and the bars represent 95% confidence intervals.

As the variances of the three foredune units were unequal (Bartlett's p-value = 0.000, < 0.05), a non-parametric Kruskal-Wallis test was used which showed a significant difference (DF = 2; p-value = 0.000, Table 2.4). The Z-values suggest a trend of decreasing density with increasing distance from the foredune face, where the Z-values of the foredune face, mid-zone and backdune face were 3.59, 0.28 and -3.87 respectively. From these values, it is apparent that the foredune face has a greater density of flower spikes m^{-2}, with the foredune mid-zone having a median density of flower spikes and the backdune face having the lowest density.

Table 2.4: A summary of the results obtained from the Kruskal-Wallis non-parametric test (DF = 2; p-value = 0.000) for the difference in flower spike density between the three foredune complex units.

Foredune unit	**N**	**Z-Value**
Foredune face	30	3.59
Foredune mid-zone	30	0.28
Backdune face	30	-3.87

2.3.2 Florets per flower spike

Similar to the density of flowering between the six depositional environments, there was a large level of variation in the numbers of florets per flower spike (Table 2.5). The number of florets per flower spike was counted for the foredune complex both as a single entity and as its three separate units. The highest mean number of florets per flower spike was seen in the foredune face (n = 483) and the lowest on the trailing arms (n = 71). Approximately half of the environments had a mean number of florets per flower spike above 200, whilst the next closest was 173.1 in the backdune sandsheets. The flower spikes of the trailing arms produced the lowest mean number of florets per flower spike (135.1). The greatest range in number of florets per flower spike was seen in the foredune face (313).

Table 2.5: Summary statistics of the number of florets per flower spike (n = 15) within the six sampled depositional environments at Mason Bay. Note: The foredune complex has also been subdivided into three separate units: 1) foredune face; 2) foredune mid-zone; and 3) backdune face, with each consisting of 15 flower spikes each.

Depositional environment	**Mean**	**Minimum**	**Maximum**	**Range**
Foredune complex	210	101	483	382
Foredune face	276	170	483	313
Foredune mid-zone	202.1	126	314	188
Backdune face	152	101	195	94
Coppice dunes	168.7	79	294	215
Northern nabkha	227.4	142	392	250
Backdune nabkha	264.7	198	372	174
Backdune sandsheets	173.1	84	346	262
Trailing arms	135.5	71	213	142

For statistical testing, the foredune complex was considered a single unit when compared against the rest of the depositional environments. In a separate statistical test, the foredune complex units were tested against each other. Figure 2.9, presents the descriptive statistics for the number of florets per flower spike in each of the six depositional environments at Mason Bay. These suggest that generally the flower spikes in both the backdune and northern nabkha produced more florets per spike compared to the other environments. The flower spikes in the coppice dunes, backdune sandsheets and trailing arms generally produced fewer numbers of florets per flower spike, whilst the foredune complex, when considered as a whole, produced a median number of seeds per flower spike. With respect to outliers, those seen in the foredune complex may be a result of the varied nature of its three single units.

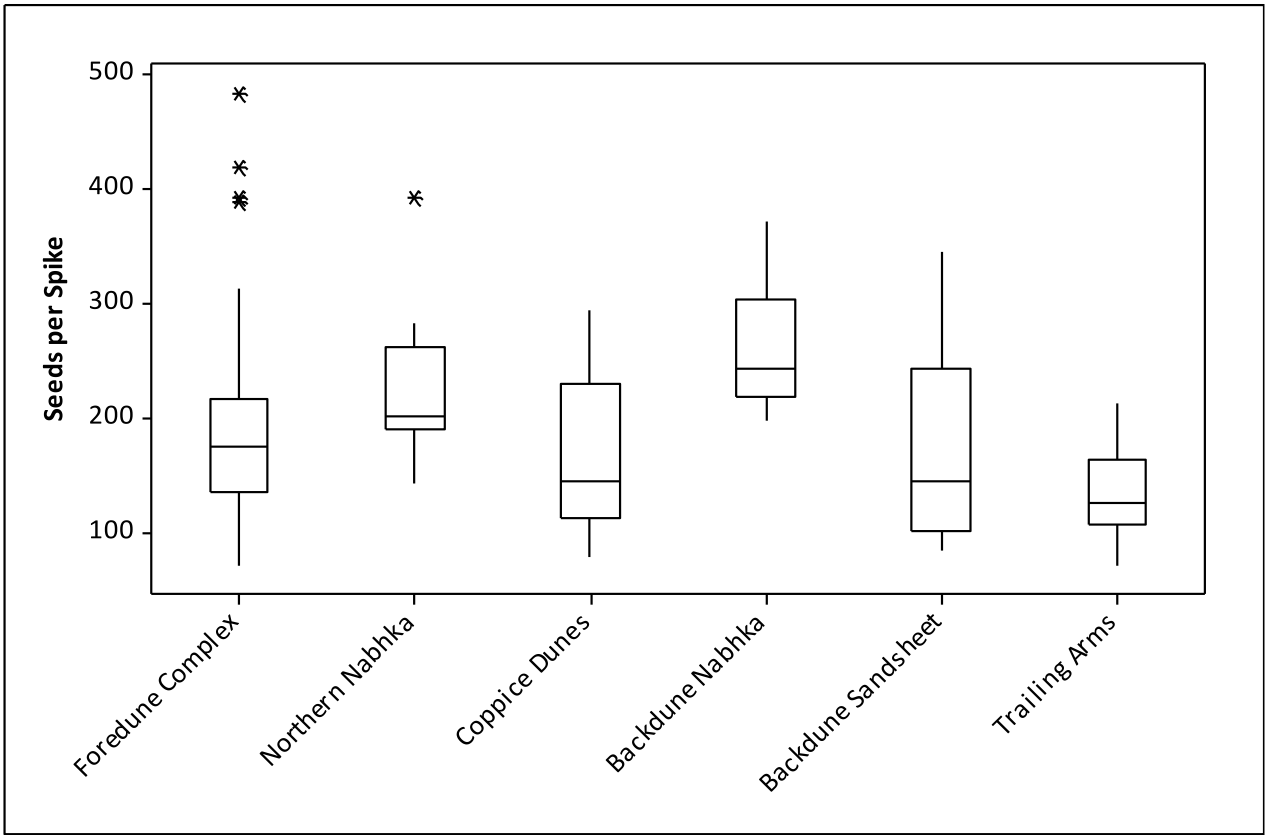

Figure 2.9: A comparison of the number of florets per spike between all six depositional environments. Note that the foredune complex has been considered as a single unit for ease of comparison against other depositional environments. For each box and whisker plot, the central line represents the mean number of seeds per spike and is bounded by the upper and lower quartiles. The stars represent suspected outliers and the bars represent 95% confidence intervals.

Testing for equal variances between the six depositional environments found that parametric testing (one-way ANOVA and Tukey's Test) was suitable for identifying any statistical significance in florets per flower spike (Bartlett's p-value = 0.062, > 0.05). A one-way ANOVA (F-value = 6.16; p-value = 0.000) showed a statistically significant difference in florets per flower spike between the six depositional environments. Tukey's posterior comparison of means suggested two statistically significant differences: 1) the backdune nabkha has significantly more florets per spike than other depositional environments except the northern nabkha; and 2) that the number of florets per flower spikes in the trailing arms is significantly less than from the backdune and northern nabkha. All other depositional environments are not significantly different from one another. In the foredune complex, the mean number of florets per flower spike decreases with increasing distance from the foredune face as well as the interquartile range (Figure 2.10).

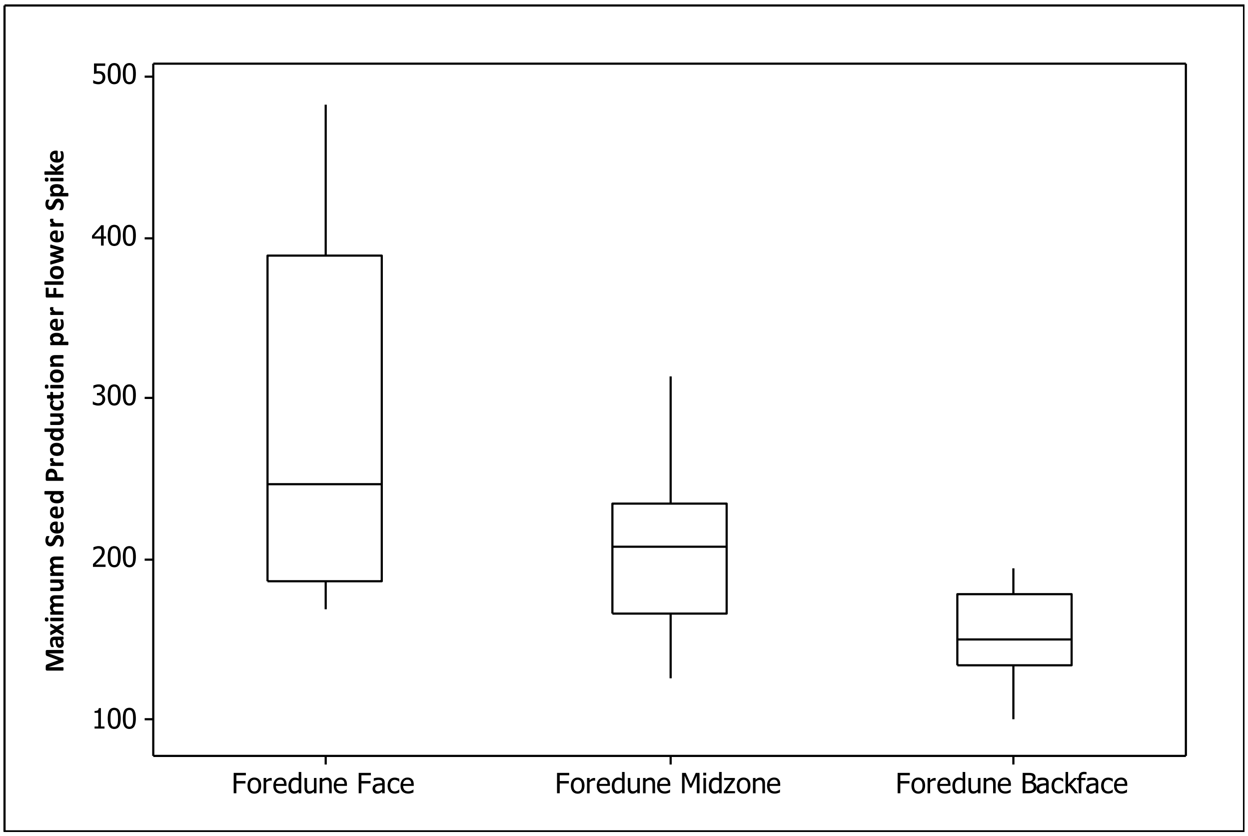

Figure 2.10: A comparison of the number of florets per spike between the units of the foredune complex. For each box and whisker plot, the central line represents the mean number of florets per spike and is bounded by the upper and lower quartiles. The stars represent suspected outliers and the bars represent 95% confidence intervals.

As the variances of the three foredune units in florets per flower spike were unequal (Bartlett's p-value = 0.000, < 0.05), a non-parametric Kruskal-Wallis test was used. The results of the subsequent Kruskal-Wallis test (DF = 2; p-value = 0.000) are presented in Table 2.6. Similar to the results obtained for the density of flower spikes m^{-2}, there was a decrease in florets per flower spike with increasing distance from the foredune face. The foredune face had the highest florets per flower spike of the three units (Z-value = 3.65), whilst the backdune face had the lowest number of florets per flower spike (Z-value = -4.02).

Table 2.6: A summary of the results obtained from the Kruskal-Wallis non-parametric test (DF = 2; p-value = 0.000) for the difference in florets per flower spike between the three foredune complex units.

Foredune unit	**N**	**Z-Value**
Foredune face	15	3.65
Foredune mid-zone	15	0.37
Backdune face	15	-4.02

2.3.3 Estimated seed crop size

Table 2.7 summarises the estimated seed crop size of the six depositional environments. The greatest seed output came from the backdune nabkha and northern nabkha, with an estimated 17,772 and 17,382.5 seeds m^{-2} respectively. The next highest potential seed output was located at the foredune face (7,691.2 seeds m^{-2}), with an output approximately 10,000 seeds m^{-2} fewer than the outputs in the nabkha environments. Both the foredune mid-zone and backdune sandsheets had potential outputs of greater than 1,500 seeds m^{-2} (2,155.7 and 1,580.4 respectively). The foredune complex, when considered as a single unit, also had a potential seed output greater than 1,500 seeds m^{-2} (2,809). The remaining environments all had much lower potential seed outputs m^{-2} (all below 300 seeds m^{-2}).

Table 2.7: The estimated seed crop size in each of the depositional environments at Mason Bay.

Depositional environment	**Density of flower spikes m^{-2}**	**Mean florets per flower spike (1dp)**	**Estimated seed crop size m^{-2}**
Foredune complex	13.4	210	2,809.3
Foredune face	27.9	276	7,691.2
Foredune mid-zone	10.7	202.1	2,155.7
Backdune face	1.6	152	243.2
Coppice dunes	0.23	168.7	39.4
Northern nabkha	76.4	227.4	17,382.5
Backdune nabkha	67.1	264.7	17,772.0
Backdune sandsheets	9.1	173.1	1,580.4
Trailing arms	1.5	135.5	196.5

2.4 Discussion

2.4.1 Introduction

Potential reproductive effort varied greatly between the six depositional environments at Mason Bay. The main factor correlated with these differences appears to be the supply of sand that is deposited in each of the environments. Marram grass is thought to rely heavily on fresh sand for not only nutrients (Maun, 1998), but also the reduction in area exposed to desiccation (Peart, 1979), amelioration of soil temperature, increases in soil moisture and organic matter (Maun, 2009) and escape from pathogens (Van der Putten et al., 1988). Other factors such as prevailing wind direction, wind speed and density of existing vegetation may also be important, because they govern the amount of sand that reaches a flowering individual.

2.4.2 Factors affecting flowering density and florets per flower spike

The backdune and northern nabkha

The two environments with the greatest estimated seed crop size were the backdune and northern nabkha (Figure 2.2). Although this was not measured directly in the study, both depositional environments were located in exposed areas of relatively high sand accumulation. At both sites, the surrounding terrain created a wind-tunnel like effect with entrained, nutrient-laden sand, being funnelled through the areas where the nabkha were located. In both these locations, there were also broad expanses of relatively bare sand situated between the nabkha and the foredune complex. This bare sand represents a significant source of fresh sediment which can be transported to the nabkha in the backdune region and provides nutrients for the vigorous growth of marram grass observed in the field. The combination of both the high volume of transported sand and funnelling of wind through the two sites creates a nutrient rich environment, ideal for a high reproductive output.

The density of the vegetation, as a result of this abundant supply of nutrients, also acts as a positive feedback. A constant supply of nutrients promotes tiller growth and a corresponding increase in density of tillers, which in turn further promotes accumulation of sand due to the increase in surface-roughness (Disraeli, 1984; Livingstone and Warren, 1996). This vigorous growth was also observed by Willis *et al.* (1959) at Braunton Burrows, England in areas of similarly extensive sand movement. Although no studies have been found looking specifically at the relationship between sand movement and reproductive vigour in marram grass, it is not difficult to ascribe an increase in available nutrients to an increase in reproductive output. Van der Putten (1990) showed that the addition of NPK fertiliser to marram grass significantly increased biomass. With respect to reproductive output, if the parent plant has a greater available supply of nutrients such as nitrogen and phosphorus, then more nutrients can be diverted from vegetative to sexual reproduction, increasing the seed crop size.

The trailing arms

The trailing arms had a significantly lower estimated reproductive output compared to the other depositional environments (Figure 2.2). This is likely the result of the moribund stands of marram grass that inhabit the trailing arms (Figure 2.11). The trailing arms originally formed when marram grass stabilised the moving sediment on the edges of the parabolic dunes and subsequently protected the less-mobile arms against wind action, allowing for the advance of the depositional lobe downwind (Livingstone and Warren, 1996). The stabilisation of these trailing arms and the subsequent reduction in sand supply, results in a marked decline in vigour and density of marram grass (the ‘ammophila problem’). This ammophila problem is characterised by a sharp decline in marram grass density, flowering, tillering, net carbon dioxide uptake, photosynthetic efficiency, rhizome production and biomass per unit area (Maun, 2009). It is thought that this decrease in vigour in the absence of fresh sand accretion probably results from a lowered rate of replacement of old roots by new adventitious roots due to competition. This may reduce marram grass’ ability to access water and nutrients (Marshall, 1965). The ammophila problem may therefore explain the significantly lower reproductive output seen in the trailing arms, as decreased vigour results in a reduced reproductive output.

Figure 2.11: The moribund stands of marram grass on the semi-stabilised trailing arms of the parabolic dunes at Mason Bay.

The backdune sandsheets

The backdune sandsheets showed an average estimated seed crop size compared to the other depositional environments. This average reproductive output suggests the intermediate nature, of the sand supply in this environment. In the backdune sandsheets, although they are situated close to the highly productive backdune nabkha, the sand supply may be partially impeded by the terrain, with Big Sandhill rising up to 156m in the backdune region. Alternatively the less dense growth of flowering marram grass populations on the sandsheets compared to the nabkha may result in less sand being deposited leading to a reduction in wind-borne nutrients. Both of these reasons may cause the lowered reproductive output seen in the backdune sandsheet environment.

The coppice dunes

Aeolian processes in the deflation surface of the parabolic dunes have eroded the relatively flat surface to a coarser, immobile layer of stones and/or the lowest seasonal water table (Carter *et al.*, 1990; Hesp, 1999). Coppice dunes form when marram grass seedlings establish either on this coarse, stony deflation surface or in conjunction with Pingao in which marram grass seed may settle, germinate and eventually displace the host (Hilton *et al.*, 2005). Both these situations initiate the trapping of sand, forming coppice dunes in an otherwise eroded environment. Once these coppice dunes have formed however, there does not appear to be enough subsequent trapping of sand to provide the nutrients necessary for a high reproductive effort. There may be two reasons for this trend.

The findings of Petersen's (2010) research into short term sand transport rates over the foredune complex at Mason Bay may explain this lack of fresh sand transport. Over the 80m - 100m long foredune complex, only aerially transported sand in suspension provided sand to the immediate hinterland behind the foredune at wind speeds greater than ~25 m/s. Calculations of total sand transport from the foredune complex to the hinterland showed between 10 to 36 kg/day^{-1} over 6 month to sub-decadal time scales. This is compared to between 513 to 1,804 kg/day^{-1} of sand transport between the beach and foredune complex. From these findings it is apparent that relatively little amounts of fresh sand is transported into the coppice dune depositional environment, which may reduce vigour in the local population of marram grass.

This lack of sand transport to the coppice dunes in the immediate dune hinterland may also be exacerbated by the sedimentation dynamics within the parabolic dune system. Depositional lobes may receive the bulk of entrained sand, with little depositing in the deflation surface and on the coppice dunes themselves. One potential reason for this lack of sand accumulation may be the absence of any significant vegetation cover on these surfaces. Observations from the field suggest that marram grass growing on the coppice dunes is often sparse, with uncharacteristically large spacing between tillers, unlike in other environments such as the foredune complex. This reduces the effects of surface-roughness normally produced by dense marram grass stands thereby reducing sand deposition in this environment. The combination of these two factors may therefore result in the low reproductive output calculated for the coppice dunes at Mason Bay.

The foredune complex

The foredune complex, considered as a single unit, showed a higher estimated seed crop size compared to the other depositional environments, except the backdune and northern nabkha. The amalgamation of the foredune complex into a single unit however hides the considerable variation between the three separate units which comprise the foredune complex (Figure 2.12). The foredune face had the third greatest estimated seed crop size (7,691 m^{-2}) compared to the other surveyed depositional environments. Similarly, the foredune mid-zone possessed the 4th highest estimated seed crop size (2,155 m^{-2}). These figures are in stark contrast to the backdune face (243.2 m^{-2}), which was considerably lower than the estimated seed crop size of the next highest depositional environment (backdune sandsheets, 1,590.4 m^{-2}) and not much higher than the lowest depositional environments, the trailing arms and coppice dunes (196.5 m^{-2} and 39.4 m^{-2} respectively).

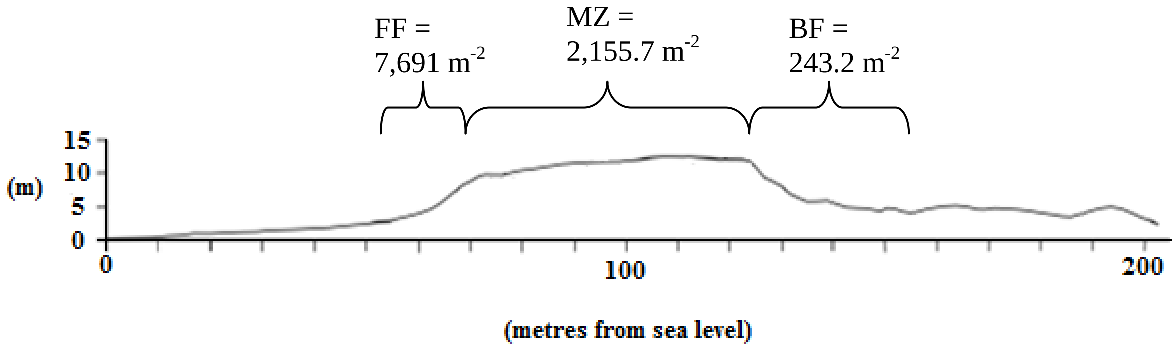

Figure 2.12: A surveyed profile of the Mason Bay foredune complex with the estimated seed crop size for the foredune face (FF), foredune mid-zone (MZ) and backdune face (BF) presented. The estimated seed crop size of the foredune complex as a single unit is 2,809.3 m^{-2}. Adapted from Petersen (2010).

These trends may be the result of a significant drop-off in sand transport in the backdune face of the foredune complex and in the immediate dune hinterland (Petersen, 2010). The results of Petersen's (2010) research also suggest that only the longest and most intense transport events, under dry antecedent conditions, enable suspension and transport of sediment of any significant distance. The low estimated seed crop size in the backdune face of the foredune therefore is likely caused by an exponential reduction in sand transport across the foredune, with deposition only likely during these high intensity events. In contrast to the backdune face, the foredune face likely receives fresh sand on a very regular basis, with Petersen (2010) suggesting that low intensity, small-scale events potentially transport sand via creep and saltation to the foredune crest but no further. These trends in sand transport under high and low intensity wind events are summarised in Figure 2.13.

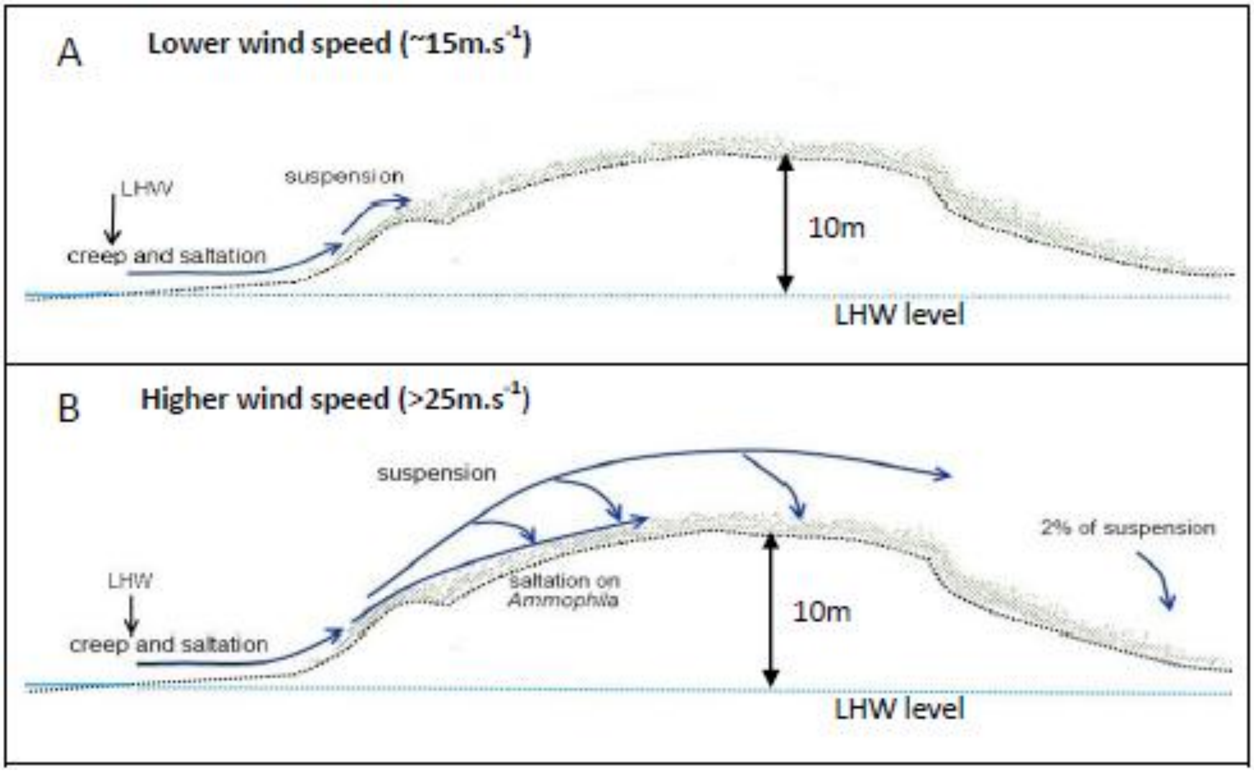

Figure 2.13: A summarisation of the modes of sand transport over the foredune complex at Mason Bay during high and low wind speeds (LHW = last high water). *Source*: Petersen (2010).

2.4.3 Estimated seed output

The combination of the density of flowering m^{-2} and florets per flower spike enables the estimation of potential seed output from each of the depositional environments. As described in the previous section, these measures of reproductive vigour are affected largely by the supply of fresh, wind-blown sand and the density of the vegetation which facilitates trapping of this sand (Maun, 2009). The upper level of production, seen in the backdune and northern nabkha (17,772 and 17,382.5 respectively), is similar to the total seed rain calculated by Rabinowitz and Rapp (1980) for a North American tall grass prairie (19,700 seeds per m^{-2}). Considering that a tall grass prairie may contain several different species over an extended area, the production in the two nabkha depositional environments indicates a very healthy population of flowering marram grass. In a subsequent study, following the 1980 seed fall, Rabinowitz (1981) showed that the subsequent seed pool contained approximately 5,640 seeds m^{-2}, indicating a dramatic loss of seeds between seed fall and incorporation into the soil environment. Similarly in marram grass, although the seed crop size estimated by this study is high in certain environments, there is likely to be a significant loss of seeds between dispersal and incorporation into the seed bank.

The comparison of marram grass production against that of a heterospecific grassland community in North America is beneficial in understanding the broad seed outputs of grasses. To put the seed output of marram grass in southern New Zealand in context however, the output obtained from Mason Bay needs to be compared against estimates of marram grass seed output from other studies. Salisbury (1952) found an average production of over 20,000 seeds per ‘clump’ per annum, and in one specific site, an output of 35,650 seeds per clump (Salisbury, 1942). These are much greater than the estimates obtained for Mason Bay and may be due to differences in methodological approach between Salisbury’s study (i.e. spatial extent of a clump) and the current study or the environment within which each Salisbury’s marram grass population was located.

Laing’s (1958) investigation of seed output in a population of *A. breviligulata*, in North America showed a flowering density of 1.3 ± 1.0 m^{-2}, a mean number of florets per head of 651 ± 152 and an estimated seed crop size of approximately 846 seeds m^{-2}. This seed crop size falls within the lower bracket of estimated seed crop sizes calculated at Mason Bay. The comparison of Laing’s (1958) data against the data of this study is perhaps most important because the method for estimating seed crop sizes during this study is similar to the approach used by Laing.

Krajnyk and Maun’s (1982) study estimated seed crop size in a population of *A. breviligulata* along the shores of Lakes Huron and Erie and found an estimated reproductive output of between 0 and 1,972 seeds m^{-2}. In comparison to the estimated seed crop sizes calculated from Mason Bay, this falls within the mid-lower range of crop sizes. Generally the comparison of the estimated seed output at Mason Bay against other studies has shown that the range of outputs calculated at Mason Bay reflect those found by other studies. However other studies estimating seed output of marram grass assumed all populations within a dune system to be homogeneous and therefore did not look at the variation of output across the dune system. In the current study, the investigation of seed output in multiple depositional environments highlights the varied nature of seed output in marram grass and, from a control perspective, indicates that some areas represent a greater risk for invasion via seed compared to others.

Determining the proportion of viable versus non-viable seeds in the estimated seed crop is an important factor in understanding the invasive potential of marram grass in southern New Zealand. Unfortunately this study did not directly quantify the proportion of viable seeds in the sampled flower spikes and very few other studies besides Laing (1958) have attempted to investigate this aspect in natural populations of marram grass. In studies of marram grass seed, viability it has often found to be low (Huiskes, 1979; Laing, 1958). However the findings of the current study have shown that germinability of healthy seeds can be approximately 82% to 94% (Chapter 3). Dispersal and invasion of marram grass via seed therefore is dependent on the proportion of healthy seeds contained on the flower spikes and the ability of seed to survive in the harsh growth conditions of the dune environment. The findings of the investigation into seedling distribution at Mason Bay (Chapter 4) however, have shown that invasion is possible in the back dune environment. This, coupled with the suggestion of some authors that even a single seedling may form a flowering satellite population in the invasion process (Esler, 1974; Laing, 1958), indicates that reproductive output from flowering stands of marram grass still poses a significant threat to dune systems.

2.5 Chapter summary

Propagule pressure plays a key role in the initiation of invasion by an invasive plant species, with increasing numbers of propagules increasing the chance of establishment. At Mason Bay, initial propagule pressure from human introduction and dispersal of rhizome via ocean currents allowed for the formation of the massive foredune complex. This provides a significant seed source for the invasion of marram grass into the dune hinterland. Following this initial invasion, new flowering populations of marram grass have formed in depositional environments. Estimating seed crop sizes from these populations represents a key area of investigation for this study and may elucidate the process of invasion by marram grass in southern New Zealand.

Six different depositional environments with flowering populations of marram grass were identified in the Mason Bay dune system (Figure 2.2): 1) the foredune complex, which was further separated into the foredune face, foredune mid-zone and backdune face; 2) the coppice dunes; 3) the trailing arms; 4) the northern nabkha; 5) the backdune nabkha; and 6) the backdune sandsheets. In order to estimate seed crop size in each of these environments, flowering density m^{-2} and number of florets per flowering spike were quantified. The results showed relatively consistent differences between the depositional environments, with the two nabkha environments showing the greatest reproductive output and the trailing arms and coppice dunes presenting the lowest output.

Although the influence of sand accretion on seed crop size was not investigated directly during the current study, it is likely that this factor played a key role in determining seed crop size between the six depositional environments. The sand supply to each of the depositional environments was affected by the local wind regime and presence of vegetation. Estimates of seed crop size developed by the study were smaller than those identified by Salisbury (1942, 1952) however later estimates by Laing (1958) and Krajnyk and Maun (1982) were within the mid to lower range compared to the estimates at Mason Bay.

This aspect of the investigation provides valuable information relating to the potential seed output in different depositional environments at Mason Bay. This is particularly important information for the control of marram grass because it indicates the potential for marram grass invasion into the dune hinterland. This information can therefore be utilised by future control programs to estimate the likelihood of marram grass invasion into dune systems.

Chapter 3

Germination of marram grass seed

3.1 Overview

Favourable conditions are required for the germination of seed, including optimal temperature, light, and moisture (Huiskes, 1977; Peart, 1979; Wesson and Wareing, 1967). These conditions are influenced primarily by vegetation cover, aspect, soil texture, burial and other variables that influence the input and retention of solar energy and moisture (Maun, 2009). Small-scale variation in temperature, light and moisture plays a key role in influencing where seeds are likely to germinate and establish. Therefore, understanding which of these factors primarily affects germination of marram grass seeds is important in elucidating the invasion process of marram grass in southern New Zealand.

The first objective of the study is to investigate the role of secondary seed dispersal in marram grass invasion in transgressive dune systems. Determining which factors affect germination and emergence in marram grass seeds is an important part in understanding where in the dune system seedlings are likely to emerge and potentially establish and is a key research question of the study (see Chapter 1). This provides a better picture of the general invasion process via marram grass seed. Therefore Chapter 3 focuses on two key aspects that are likely to affect germination and the subsequent emergence of marram grass seedlings in coastal dune environments: 1) the effects of light and darkness; and 2) the effects of burial.

3.2 The effects of light and darkness on germination

The effects of light and darkness on seed germination have been investigated in several studies. The findings of Wesson and Wareing (1967) suggest that a light requirement may be the most important factor regulating the dormancy of buried seeds. However in their tests using fresh seed, it was found that light was not the principal factor in determining germination, with the authors later suggesting that burial may modify this requirement. In a subsequent study of 11 weed species germinated after 50 weeks of burial, no germination was observed in the absence of light (Wesson and Wareing, 1969a). Testing of germination under natural field conditions also showed a complete dependence on light for germination at all depths of burial (Wesson and Wareing, 1969b). A study by Van der Putten (1990) found similarly that germination of marram grass seeds in darkness was generally lower than germination in light. This was also found to be temperature-dependent, however it was suggested that this germination may have been an artefact caused by the use of a green safety light during watering and counting (which will be discussed later). In the constantly shifting substrate of the coastal dune environment the requirement for light may therefore play an important role in determining marram grass germination.

3.3 The effects of burial on germination

Burial acts as a strong selective force in the coastal dune system and drives species composition of sand dune communities on a local scale (Forey et al., 2008). Baskin and Baskin (1989) state that the primary reason seeds do not germinate while buried is that many have a light requirement before germination can take place. Studies investigating the effects of burial on seed germination have found that shallow depths, i.e. 1mm, improve the rate of germination compared to bare surfaces (Van der Meijden and van der Waals-Kooi, 1979). It is also generally accepted that as burial increases past 4mm – 5 mm, germination is inhibited (Tester and Morris, 1987). Suggested mechanisms for the inhibition of germination include the lack of light penetration to depths at which seeds are buried or changes in temperature which may directly affect the ability of the seed to germinate (Tester and Morris, 1987; Woolley and Stoller, 1978). In Mott's (1978) investigation of dormancy and germination in native grasses of the Northern Territory, Australia, burial was found to benefit seeds by vertical movement away from the soil moisture and temperature extremes of the surface as well as increasing seed-soil contact for water uptake. Morphological features such as sharply pointed calluses and hygroscopically active awns (similar to marram grass) also aided in the vertical movement of seeds away from these extremes of the desert surface. Although burial offers several benefits with respect to ameliorating microenvironmental conditions, germination and emergence of seedlings may be inhibited by the onset of dormancy in buried seeds. It is therefore important to investigate the response of marram grass seed to burial and the implications this has for the invasion process in southern New Zealand.

3.4 Method

3.4.1 Study site – Oreti Beach

Oreti Beach is located in the vicinity of Invercargill on the southern coast of the South Island (Figure 1.5). Oreti Beach is a broad, flat, dissipative beach with a narrow set of dune ridges dominated by introduced marram grass (Robertson and Stevens, 2008). Its location on an exposed west-facing coast results in episodic sand deposition during strong onshore winds which leads to the formation of a series of dune ridges parallel to the ocean (Hilton, 2000), similar to those found at Allans Beach (Chapter 5). This deposition of sand benefits seed production through the provision of a constant source of nutrients (Huiskes, 1979), making Oreti Beach an ideal site for the collection of marram grass seed.

3.4.2 Seed collection and preparation

All of the seeds used for the germination trials in this study were collected from Oreti Beach on February 18th 2010. This date was estimated to coincide with the completion of seed maturation in southern New Zealand (Pope, 2005). After collection, the seeds were air dried for one week before undergoing cold stratification. The cold stratification treatment began on February 25th 2010, where seeds were placed in a refrigerator at 6.5°C with a relative humidity of 76%. This cold stratification treatment ended when seeds were prepared for their respective germination trials. Before germination experiments testing the effects of light and darkness and burial on the germination of marram grass seed could be carried out however, the percent germinability and viability of the Oreti Beach seed had to be ascertained. This gave an indication of the background rate of germination that could be expected during trials.

3.4.3 Percent germinability

In order to test percent germinability, 100 seeds were divided evenly between four 90mm Petri dishes (which were used throughout the study) which had been lined with Whatman No. 3 filter paper and watered with distilled water. The replicates were then exposed to a germination treatment of a fluctuating temperature regime and a 14 hour photoperiod (22°/15°C; 14h/10h) following Hendry and Grim (1993), as a simulation of late spring/early summer conditions. The process of cold stratification followed by a warm germination treatment was chosen because it generally reflects the life cycle of marram grass seed in Europe, which disperses in summer, is buried and stratified in winter and emerges in spring with increasing temperature and available moisture (Huiskes, 1977). Due to the wide range of marram grass over Europe, it was considered that this treatment would also be sufficient to trigger germination in marram grass seed from southern New Zealand. The first percent germinability experiment commenced on May 13th 2010 (7 weeks of cold stratification) and was conducted over 60 days, with daily watering of seeds. Germination of seeds was recorded upon emergence of the radicle (Bosy and Reader, 1995; Gulzar and Khan, 2001).

Over the course of testing for germinability, three separate treatments were eventually conducted. The initial ‘no treatment’ test for germinability showed no germination from the tested seed within the first 34 days. In order to comprehensively test germinability, two other treatments were begun on the 8th of June 2010 (10 weeks of cold stratification) to run concurrently with the ‘no treatment’ test. These were: 1) a ‘double filter paper’ treatment, which involved placing seeds between two pieces of moistened filter paper (Figure 3.1); and 2) a ‘no outer structures’ treatment, where the palea and lemma of the seed were removed, leaving only the exposed caryopsis (Figure 3.2). Both treatments contained the same number of seeds and were germinated under the same environmental conditions as the ‘no treatment’ experiment. These two further treatments were deemed necessary because lessons had been learnt as to the correct amounts of water needed for vigorous germination during the first experiment. It is suspected that initially not enough water was applied to the ‘no treatment’ replicates resulting in the continuous wetting and drying of seed, which generally impedes germination (Gosling, 2003). Therefore, in the two subsequent treatments, sufficient moisture was applied on a daily basis to keep the filter paper moist. Care was also taken to not partially or fully immerse seeds in water as this has also been shown to reduce aeration and impede germination (Gosling, 2003). The latter two treatments were carried out for 44 days until cessation of germination. The ‘no treatment’ experiment was carried out over 60 days in order to end at the same time as the other two treatments.

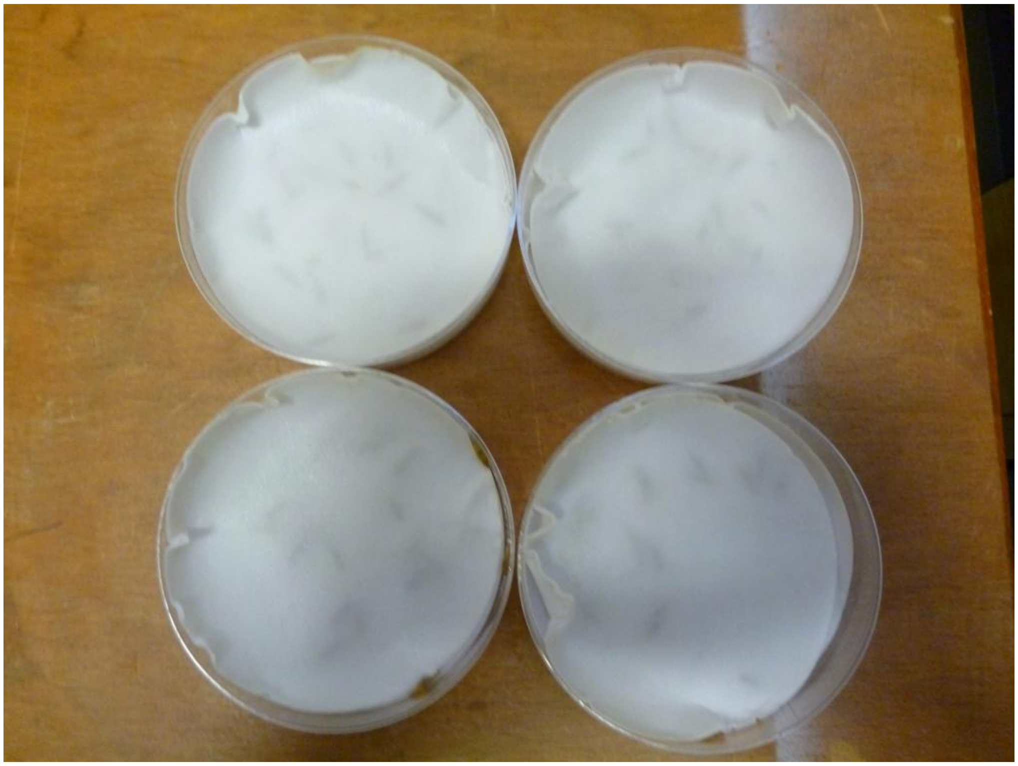

Figure 3.1: The double filter paper treatment for testing seed germinability.

Figure 3.2: Exposed caryopses following the removal of palea and lemma for the no outer structures treatment for testing seed germinability.

3.4.4 Tetrazolium tests for viability

The determination of viability using chemical tests was undertaken as a parallel line of enquiry to better understand not only the germinability of the marram grass seed but also the potential viability. Percent viability was tested using triphenyl-tetrazolium chloride (henceforth tetrazolium chloride) which stains the seed a pink-red colour where mitochondrial function has resulted in the reduction of tetrazolium chloride to a non-diffusible formozan (Freeland, 1976). The method described for percent viability testing was adapted from Freeland (1976).

Seed viability tests were conducted on 100 seeds on the 17th of November 2010 following 38 weeks of cold stratification. This was not considered to have greatly affected the viability of stored seed, especially when considering the longevity and viability of the marram grass seed bank (Chapter 5). Before staining could commence, seeds needed to imbibe distilled water over a 12 to 24 hour period. This was done by placing 25 seeds into four Petri dishes with moistened filter paper and these were left overnight in a dark store room. A 1% solution of tetrazolium chloride was then prepared by dissolving one gram of powdered tetrazolium chloride salt in 100ml of distilled water. Seeds were surface sterilised using a cleaning solution of 10ml of bleach to 100ml of water, in order to reduce the chance of false positives from any living organisms on the seed surface (Pope, 2005). The instruments used to prepare seeds were also sterilised in this cleaning solution between the preparations of each seed for staining.

The seeds were cut in half longitudinally using a sterile scalpel and each half was placed in separate Petri dishes to ensure that the embryo of the seed had the chance to be stained. During the cutting process, because the embryo could end up on either half of the seed, testing of both halves was carried out to minimise any error associated with a missed result (Figure 3.3). After cutting, the seeds were then soaked in the 1% tetrazolium chloride solution for 24 hours in a dark store room to allow for staining to take place. Seeds were then checked for staining under a dissection microscope. Although a pink-red colouration denotes mitochondrial activity, it does not necessarily indicate viability. Generally the intensity of the colouration is related to the number of mitochondria present and therefore the activity of dehydrogenase (Freeland, 1976). Seeds perceived to be viable (a positive result) will show a much greater intensity of colour around the embryo and positive results were those deemed to show an intense colouration in this region (Figure 3.4).

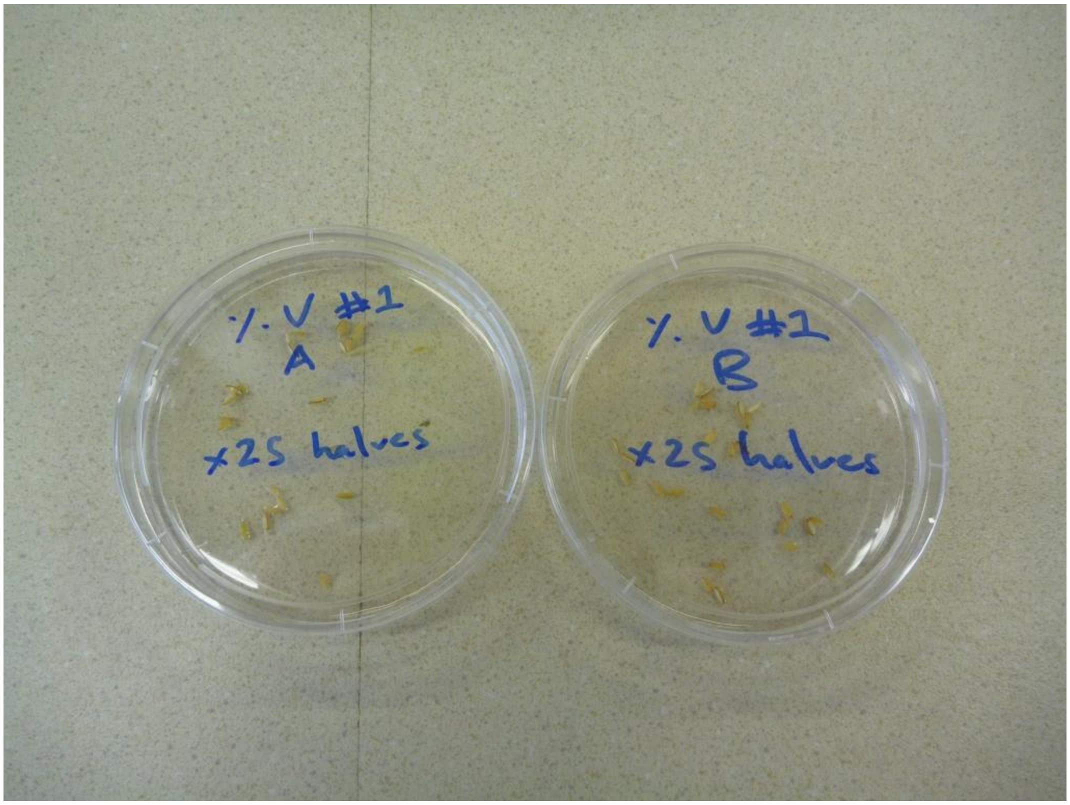

Figure 3.3: An example of the seed halves divided between two Petri dishes.

Figure 3.4: A comparison of a positive (left) and negative (right) staining result.

The purpose of investigating both percent germinability and viability was to determine the background rate of germination that could be expected when conducting the light versus darkness and burial germination experiments. It also served to identify which seed pre-treatments i.e. the removal of the lemma and palea, resulted in the greatest rate of germination. Most importantly, this informed the method for germinating seeds, collected during the coring process of the seed bank longevity investigation (Chapter 5), to ensure that the maximum possible rate of germination could be achieved.

3.4.5 Light versus dark

In the comparison between germination under light and dark conditions, 100 seeds were evenly divided between four Petri dishes for both treatments. Those replicates used in the light treatment were then subjected to the same conditions as the percentage germinability tests (section 3.4.3). The dark replicates were initially placed in single layer black cloth bags (Figure 3.5), to exclude light, and these were placed in the same *Contherm Plant Growth Chamber* as the light treatment. In order to inspect the replicates for germination, checking and watering was initially carried out under a red safe light (this treatment will henceforth be called dark red). Red light however was found to stimulate germination in marram grass seeds and therefore the experiment was re-started after 19 days using a green safe light for inspections.

The second dark experiment (henceforth called dark green) also included a change in bagging treatment, where the Petri dishes were placed inside two layers of black cloth bags to further exclude light. Again, germination of seeds was recorded upon emergence of the radicle (Bosy and Reader, 1995; Gulzar and Khan, 2001). The light and dark red experiments commenced on August 12th 2010 (20 weeks cold stratification) and the dark green experiment began on 3rd September 2010 (24 weeks cold stratification). The light and dark green treatments were intended to be carried out over a 42 day period following Pope's (2005) method however the light treatment was extended to 48 days due to continued germination. At the cessation of the 42 day period in the dark green treatment, the remaining seeds were then exposed to the same conditions as the light treatment for 21 days (henceforth called dark green + light) and the rate of germination was recorded. The dark red experiment did not undergo this additional light treatment.

Figure 3.5: The light and dark treatments in the *Contherm Plant Growth Chamber*.

3.4.6 Emergence from burial

Four burial treatments of 5 cm, 10 cm, 15 cm and 20 cm and a control depth of 0.5 cm were selected to investigate the ability of marram grass seed to germinate and emerge from burial. This method is similar to that of Greipsson and Davy (1996) who investigated emergence from burial of the coastal grass *Leymus arenarius*. Each treatment consisted of three replicates of a 25 cm deep square polythene bucket with five holes drilled into the base to allow for drainage of water. A layer of curtain netting was laid over the holes before filling with sand in an attempt to reduce sand loss through the drainage holes. The experiment was initially setup using horticultural sand, however after several weeks it was decided that, during watering, horticultural sand compacted and inhibited emergence in marram grass seed. This did not reflect conditions associated with burial by coastal sand and resulted in the re-starting of the experiment. In the second attempt, buckets were setup as before, however washed beach sand was used to bury the seeds. At the base level of burial, a double layer of curtain netting was laid across the sand surface to prevent seed movement deeper than the prescribed burial treatment. The seeds were then evenly spaced across the surface of the netting and buried according to the appropriate burial treatment (Figure 3.6). The treatments were commenced on the 27th of September 2010 (after 30 weeks cold stratification), stored in a greenhouse and watered daily over a 42 day period.

Figure 3.6: A 20 cm burial replicate with seeds laid evenly over the netting surface.

After 42 days, each replicate was manually excavated to recover all of the buried seeds. Seeds were classed according to one of three anticipated fates: 1) germinated and emerged; 2) germinated but not emerged; and 3) had not germinated. Those seeds that had already emerged before the end of the 42 day period were recorded and removed. Any recovered seeds that had not germinated were transferred to a Petri dish with moist filter paper and placed in a *Contherm Plant Growth Chamber* under the same growth regime as the test for seed germinability (section 3.4.3). The seeds remained under these conditions for two weeks to test for germinability when exposed to light. After two weeks any remaining ungerminated seeds were tested for viability using the tetrazolium method described in section 3.4.4.

3.4.7 Statistical analysis

Prior to statistical testing, the light and dark treatment data was tested for equal variances using a Bartlett's test. This confirmed that parametric testing was suitable and therefore a one-way ANOVA test was used to compare the three different light and dark treatments. All statistical analysis was carried out using Minitab 15. Unfortunately data from replicate Petri dishes or buckets was not recorded separately for the germinability or burial treatments, precluding the use of analysis of variance.

3.5 Results

3.5.1 Seed germinability

As previously described in this chapter, in order to test germinability of the seed collected from Oreti Beach, three separate methods of germination were employed. The results of these experiments are summarised in Table 3.1 and presented graphically in Figure 3.7. The first test of germinability, in which no treatment to seed or modification of germination method occurred, had a much lower percent germination (28%), compared to the 'double filter paper' and 'no outer structures' treatments (82% and 94% respectively). It also had a much greater experimental length (60 days) compared to the other treatments (both 44 days). The low percent germination may have arisen largely from the initial inexperience of the researcher in germinating marram grass seed. This affected the length of the experiment (60 days compared to 44 days) because extra time was required to gauge what germination could be obtained using methods learnt during the latter two treatments.

Table 3.1: The percent germination of seed collected from Oreti Beach under constant environmental conditions but with differing germination methods.

Treatment	**No treatment**	**No outer structures**	**Double filter paper**
Percent germination	28	94	82
Days until 50% of germination	22	18	19
Length of experiment	60 days	44 days	44 days

The ‘no outer structures’ treatment showed a higher percent germination after the 44 day period (94%) compared to the ‘double filter paper’ treatment (82%) however, there did not appear to be a great difference in rate of germination with both treatments reaching 50% of germination in 18 and 19 days respectively. This is highlighted in Figure 3.7, with both the blue (no outer structures) and green (double filter paper) lines roughly following a similar pattern of germination. These results give an indication of the germinability of seed used to investigate phenomena such as light versus dark effects on germination and emergence of seed from burial.

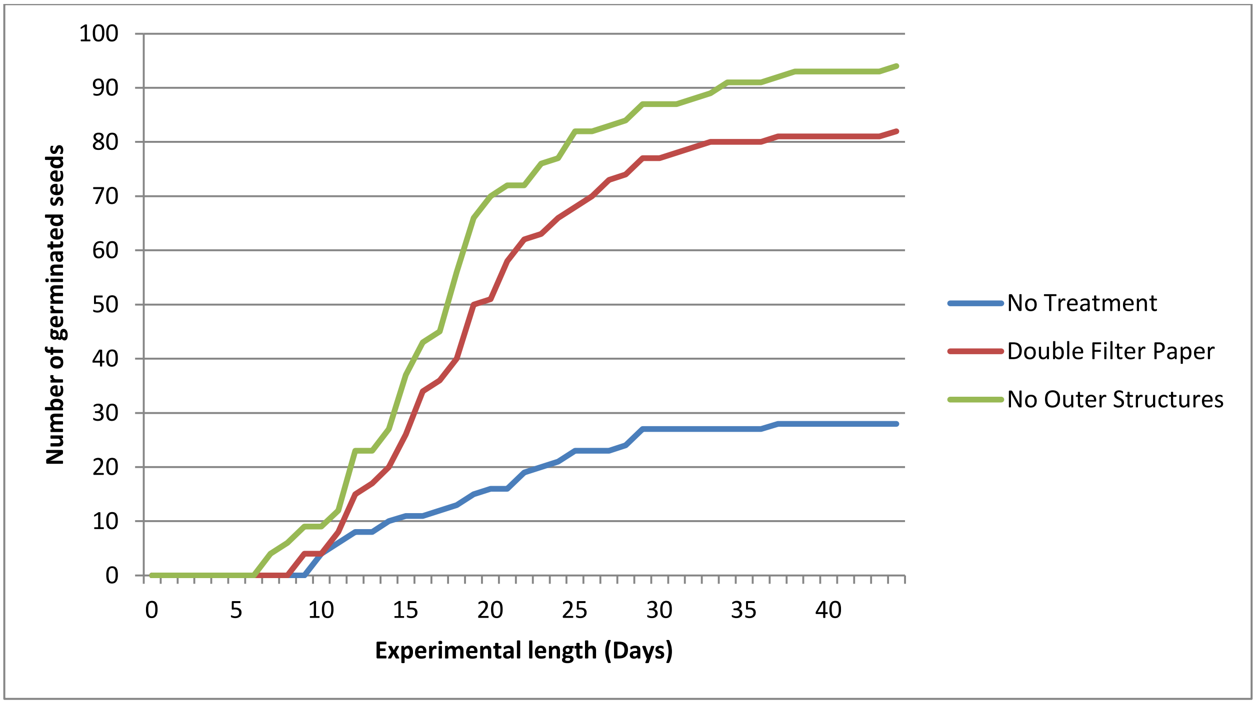

Figure 3.7: The rates of germination of seeds collected from Oreti Beach using the three different germination methods. Note that the 'no treatment' experiment was carried out over 60 days rather than 44 days however for the benefit comparison a common baseline is used.

3.5.2 Tetrazolium tests for viability

One hundred seeds in four replicates of 25 seeds each were tested for percent viability using tetrazolium chloride. The percent viability in the four dishes ranged from 48% to 64% or 12 to 16 positive results out of 25 seed halves respectively. This produced an overall seed percent viability of 58% (Table 3.2). Although this is higher than the percent germinability found in the 'no treatment' experiment (28%), it is significantly lower than the 82% and 94% germinability of the other two treatments.

Table 3.2: A summary of the results from each of the replicates used in the test for percent viability. The number of seeds, positive results and negative results as well as the percent viability of each replicate is presented, along with the overall percent viability across all four dishes.

Dish #	**1**	**2**	**3**	**4**	**Overall percent viability**
Number of seed	25	25	25	25	
Positive results	15	16	15	12	
Negative results	10	9	10	13	
Percent viability	60	64	60	48	58

3.5.3 Light versus dark

The four treatments showed some variation in percent germination and the time taken until 50% germination (Table 3.3). The light treatment had a relatively high percent germination compared to the other treatments (68%) with only the fourth treatment, ‘dark green + light’, having a higher percent germination (70%). In contrast to the light treatments, the dark red and dark green treatments showed a much lower percent germination (42% and 33% respectively). Statistical analysis comparing the light, dark red and dark green treatments was carried out in order to determine if there were any statistically significant differences between percent germinability and the time taken to reach 50% germination between the three treatments. Testing for equal variances confirmed that parametric testing was suitable for the comparison of percent germinability (Bartlett’s p-value = 0.618). A one-way ANOVA for percent germination ($F_{2,11}$ = 11.3; P =0.004) indicated a significant difference exists between the treatments. Group means compared using Tukey’s tests confirmed that the light treatment was significantly different compared to the dark treatments.

The time taken to reach 50% germination was faster in both the dark treatments compared to the light treatment with 15 days and 13 days required respectively compared to 21 days. This may however have been related to the lower overall percent germination in the dark treatments, which allowed 50% of germination to be reached sooner. Testing for equal variances confirmed that parametric testing was suitable for statistical analysis (Bartlett’s p-value = 0.535). A one-way ANOVA for time taken to reach 50% of total germination ($F_{2,11}$ = 20.63; P < 0.000) showed that a significant difference exists between the treatments. Group means compared using Tukey's tests also confirmed that the light treatment was significantly different to the dark treatments.

Table 3.3: A summary of the total number of seeds that germinated, percent germination, the time taken to reach 50% germination and the length of each experiment for the four light and dark treatments.

Treatment	**Total no. of seeds**	**Total no. of germinated seeds**	**Percent germination**	**Days until 50% of germination**	**Length of experiment**
Light	100	68	68	21	42 days
Dark red	100	42	42	13	19 days
Dark green	100	33	33	15	42 days
Dark green + light	67	47	70	11	21 days

The fourth treatment, 'dark green + light' began after 42 days and is represented in Figure 3.8 after the 42 day mark as part of dark green treatment (green line). This method of presentation was used to highlight the rapid change in rate of germination and the overall level of germination seen in the seeds of this treatment after exposure to light. Table 3.3 highlights this trend with an overall percent germination of 70% (47 of 67 seeds germinated) in the 'dark green + light' treatment compared to the 33% percent germination of the dark green treatment (33 of 100 seeds germinated). The rate of germination was also much more rapid after exposure to light, with 50% germination being reached after 11 days in the 'dark green + light treatment' compared to 15 days for the dark green treatment. Over the 21 days of the 'dark green + light' treatment, the rate of germination was relatively rapid compared to the other treatments however this rate tailed off significantly on the 23rd of October 2010.

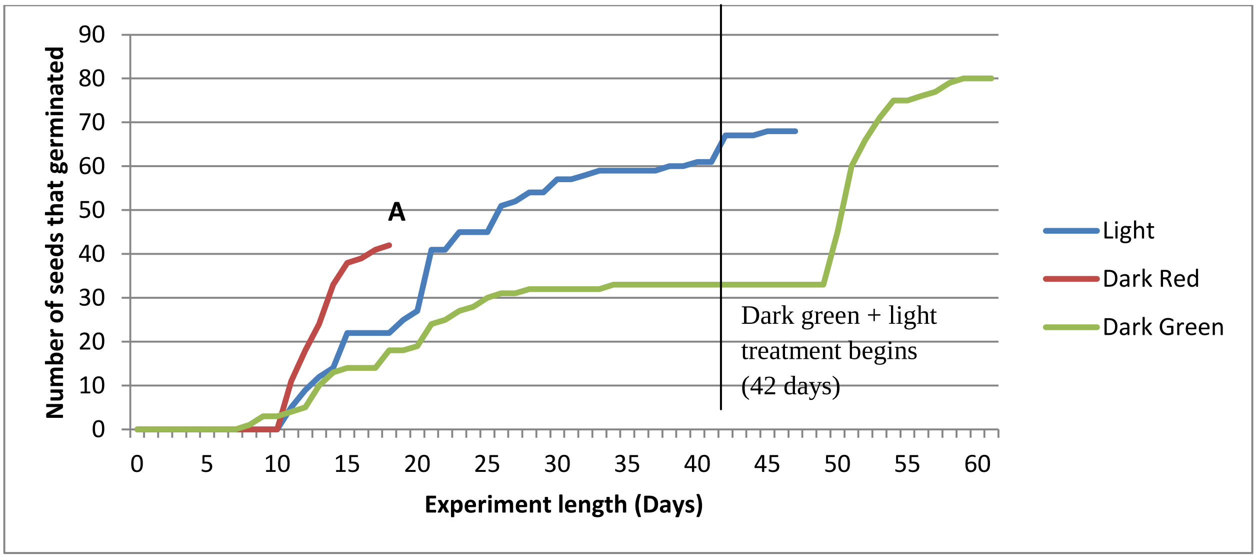

Figure 3.8: A comparison of the rates of germination for seeds treated under light conditions and dark conditions. The rate of germination is shown for seeds germinated under light and dark conditions with both the red and green safety lights. The dark green + light treatment begins on day 42 after the vertical line. 'A' = Dark red experiment ceases.

3.5.4 Emergence from burial

The five burial treatments, with the exception of the control (0.5 cm burial depth), showed little to no emergence from burial by marram grass seedlings (Figure 3.9). Emergence was only recorded in the control depth (0.5 cm, blue line) and 5 cm (red line) burial treatments. In the control treatment, the total number of seedlings that emerged from burial was 24, representing 29% of the 75 seeds originally buried. In the 5 cm treatment, a total of three seeds emerged, representing 4% of the 75 seeds originally buried. The time taken to reach 50% of total emergence was similar for the control and 5 cm treatments (29 days and 31 days respectively). Initial emergence of seedlings in the two successfully emerged treatments occurred after similar time lapses of 20 and 23 days respectively. There was no emergence recorded in any of the other burial treatments (Table 3.4).

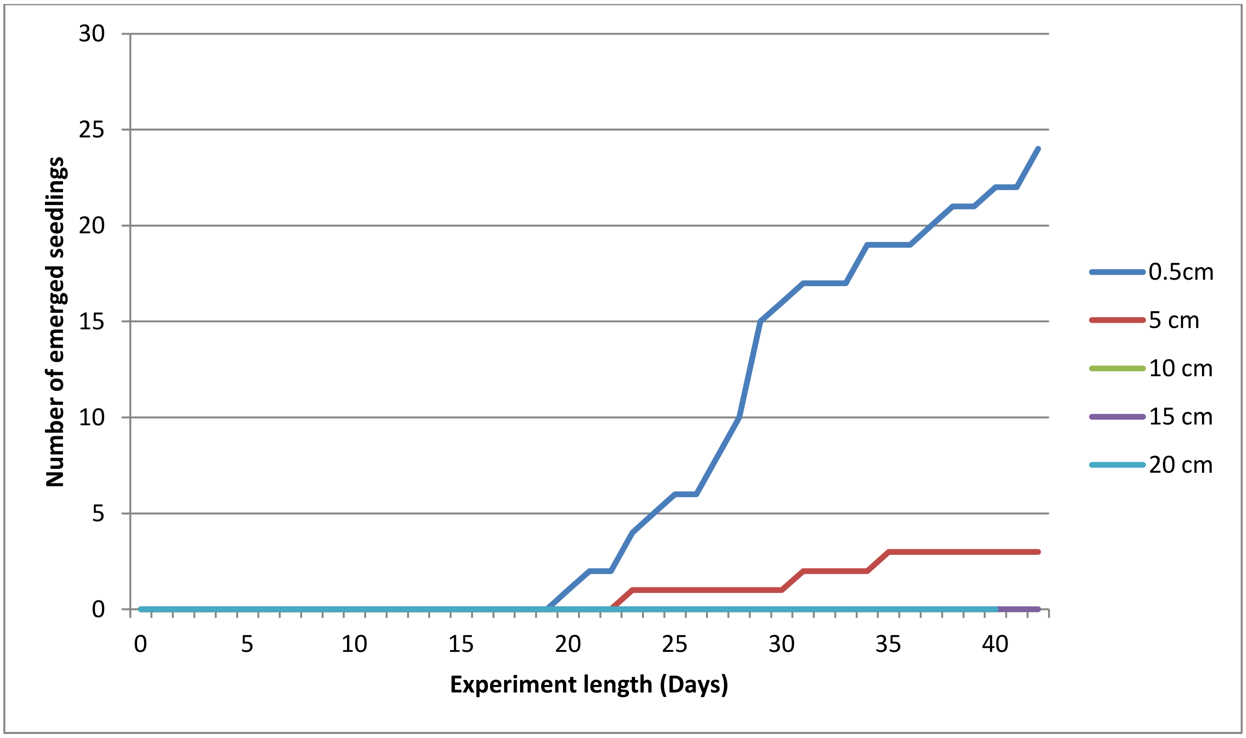

Figure 3.9: The rate of emergence of seedlings from the five burial treatments.

Once the emergence treatments had been carried out over the full 42 day period, each replicate was carefully excavated in order to recover buried seed and to assess seed fate following burial. This data is also presented in Table 3.4. Initially it was thought that all of the recovered seeds that had germinated had also subsequently emerged. However, during viability testing of seed using tetrazolium chloride, some seeds were found to have germinated but the radicle had not penetrated the glumes. Within each treatment, there were a total of 75 seeds (or 25seeds per replicate) but not all of these seeds were able to be recovered, for reasons discussed in section 3.6.4. The highest level of recovery from any treatment was 80%, in the 20 cm treatment, with the lowest being 41.3% in the 5 cm treatment. In two of the five treatments, the rate of recovery was less than 50% representing a much lower level of seed recovery than was expected.

Table 3.4: A summary of the emergence and excavation results for the five burial treatments conducted on seed collected from Oreti Beach.

Treatment	Control 0.5 cm	5 cm	10 cm	15 cm	20 cm
Total emergence	24	3	0	0	0
Percent emergence	29.3%	4%	0	0	0
Days until 50% of total emergence	29	31	N/A	N/A	N/A
Length of experiment	42 days	42 days	42 days	42 days	42 days
Total seeds recovered	58	31	44	33	60
Percentage of seeds recovered	77.3%	41.3%	58.7%	44%	80%
Total seeds recovered but not emerged	34	27	44	33	60
Total seeds emerged	24	4	0	0	0

After excavation, the seeds were germinated over a two week period beginning on the 19th of November 2010, with the results summarised in Table 3.5. The 0.5 cm treatment showed the lowest percentage germination (79.4%) whilst the highest percentage germination was seen in the seeds excavated from the 15 cm treatment (90.9%). With respect to the time taken until 50% germination, the 0.5 cm, 5 cm and 15 cm treatments all took 10 days whilst the 10 cm and 20 cm treatments took 11 and 9 days respectively. This suggests a similar rate of germination with the greatest difference in time taken being two days between any two treatments.

Table 3.5: A summary of the results from the germination of excavated but ungerminated seeds. The total number of seeds, total germination, percent germination, time taken until 50% of germination and length of experiment are presented.

Treatment	Control 0.5 cm	5 cm	10 cm	15 cm	20 cm
N	34	27	44	33	60
Total germination	27	24	35	30	52
Percent germination	79.4	88.9	79.5	90.9	86.7
Days until 50% of germination	10	10	11	10	9
Length of experiment	14 days	14 days	14 days	14 days	14 days

Following the test for germinability of excavated seeds, percent viability was also tested, to ensure a more complete understanding of the condition of the ungerminated seeds. The results of this investigation are presented in Table 3.6. It should be noted that all of the burial treatments, except 15 cm, contained a few individuals that were either dead or had been attacked by fungi and/or mould and were excluded from testing. Further to this, any seeds that were found to have germinated inside their casings were added to the germination tally as they were considered germinable. Five seeds in the 10 cm treatment and one seed in the 15 cm treatment were found to have germinated and these results have been added to their respective germinability counts in Table 3.5. Seeds from all burial treatments, except 20 cm, showed percentage viability greater than 50%. The four seeds tested for percentage viability from the 20 cm treatment however showed no viability.

Table 3.6: The results of the percent viability tests of seeds that were excavated from the burial treatments but did not germinate after 14 days under optimal germination conditions.

Treatment	Original number of seeds	Seeds dead or attacked by fungi/mould	Number of tested seeds	Number of positive results	Percent viability	Germinated seeds
0.5 cm	7	4	3	2	66.7%	0
5 cm	3	1	2	1	50%	0
10 cm	9	1	8	7	87.5%	5
15 cm	3	0	3	3	100%	1
20 cm	8	4	4	0	0%	0

3.6 Discussion

3.6.1 Seed germinability and viability

Testing the germinability and viability of seed collected from Oreti Beach showed a disparity between the different methods used to determine the overall viability of seed. Due to initial issues with the ‘no treatment’ experiment, the latter two treatments provided a better idea of the germinability of seed. Seed germinability was found to range between 82% and 94% (the ‘no treatment’ results are not included here because of methodological issues), whilst testing with tetrazolium chloride produced a seed viability of 58%. Pope (2005) carried out a similar investigation in which fresh, dried and stratified marram grass seed from two separate years (2004 and 2005) was tested for germinability and fresh seed (2004) was tested for viability using tetrazolium chloride. The results of his germinability testing were much lower compared to the findings of the current study (Table 3.7). In contrast, the viability of the fresh seed collected in 2004 (the most viable year in Pope's study) was shown to be 57.5% for marram grass which is comparable to the results of the current study. Pope suggested that the disparity in his study between germinability and viability of seed may be due to the exhibition of innate dormancy in marram grass seed or sub-optimal seeds which are metabolically active but not able to germinate.

Table 3.7: A summary and comparison of the findings of Pope's (2005) and the current study's research into the germinability and viability of marram grass seed.

	Percentage germinability		**Percentage viability**
	2004	**2005**	
Fresh Seed	40.08%	15.9%	57.5%
Dried Seed	7.37%	7.75%	N/A
Stratified Seed	2.91%	11.82%	N/A
Oreti Beach Seed (2010)	82% - 94%		58%

Van der Putten (1990) tested the germinability of marram grass seed that had been collected from Voorne Island, Netherlands in July 1986 and stored dry for 5 months at 12°C. These seeds were then stored at 4°C with demineralised water (stratification treatment) or kept dry for 0, 2, 3, 5 or 7 weeks as a pre-treatment. The study found that the effect of pre-treatments depended on germination temperature, with fluctuating rather than constant temperature regimes having the best germination results. After five to seven weeks of cold stratification, an incision in the seed coat and a period of germination of 22 days (10/20°C; 16h/8h), marram grass seed showed 94% germinability. When daily fluctuating temperatures were increased (20/30°C; 16h/8h), 80% germinability was observed in marram grass seed after 10 to 15 days. These results generally reflect those of the current study however no testing of seed viability using tetrazolium was conducted by Van der Putten (1990).

In studies investigating the viability of seeds of other plant species using both germination and tetrazolium chloride tests, seed viability was generally found to be greater than germinability.

Bell et al. (1995) in their study of 43 Western Australian plant species with varying life-history strategies found that the average overall seed viability was 71% compared to a mean maximum germinability of 45%. In nearly all cases, the maximum mean germination was less than the viability of the seeds of a particular species, a trend which was attributed to seed dormancy. Chacalis and Reddy (2000), in their investigation of the factors affecting germination in *Campsis radicans* seed, found that without a pre-chilling treatment, maximum germination was 17% compared to seed viability of greater than 90%. With pre-chilling treatments however, germinability of *C. radicans* seed increased to 74% emphasising the importance of dormancy-breaking pre-treatments in improving germination. In contrast to this trend, Harty and McDonald (1972) found that the viability of seed of the sedge Spinifex (*Spinifex hirsutus*) was 80% compared to a germinability of 78% and 79% under 15/25°C and 20/35°C treatments respectively (Harty and McDonald 1972). While the findings of Harty and McDonald (1972) do not reflect those of the current study, it does suggest that the viability of seed will not always be significantly greater than germinability of seed.

The disparity between seed viability and germinability found in this study may have been caused by two reasons. Firstly, error associated with the inexperience of the researcher may have resulted in inaccurate readings of stained seeds when testing for viability. Gosling (2003) notes that the use of tetrazolium as a chemical test for viability requires practice in both preparation and interpretation. Often a species will have its own specific idiosyncrasies making the identification and differentiation of positive and negative results difficult without practice.

However, the more likely reason for the disparity is the extended period of cold stratification that the seeds underwent before viability testing compared to the tests for germinability. Although it was initially considered that the long cold stratification pre-treatment did not affect seed viability, citing the results of the seed bank longevity results (Chapter 5), the artificial storage conditions inside the refrigerator may have resulted in a faster rate of decay. Chacalis and Reddy (2000) noted that, although pre-chilling for 2 weeks improved germination of seed, after four months, germinability had decreased from 74% to 10% in *C. radicans* seeds. This highlights the need for caution in future studies when conducting germinability and viability testing. Conducting both tests concurrently rather than separately, as was done in this study, may also provide more accurate results. Generally however, the results obtained from the germinability and viability tests suggest that the Oreti Beach seed was of a relatively high germinability when testing the effects of light and darkness and burial on marram grass seed.

3.6.2 The effects of light and darkness on germination

Testing for light sensitivity in marram grass seed showed a greater rate of germination in seeds exposed to light compared to those germinated in darkness under weak green and red light. Van der Putten (1990) also investigated germination of marram grass seeds in darkness using light-proof bags (germination was checked using a green safe light) and found that although there was some germination, generally it was significantly lower than germination in the light treatments. However an exception was seen in marram grass seed that had undergone cold stratification for five to seven weeks and was germinated under fluctuating temperatures (10/20°C; 16h/8h) where percentage germination ranged between 60% and 90% respectively. The only explanation offered for this phenomenon was that it may have been an artefact caused by the use of the green safe light. The results of Van der Putten (1990) and the current study suggest that marram grass seed is very sensitive to light, with germination potentially being initiated by two scenarios: 1) a strong, innate sensitivity to even weak green or red light possessed by marram grass seed; and/or 2) that seeds may have reacted to artificial and natural light exposure during preparation for germination in the dark.

One potential cause for the relatively high germination response in marram grass seeds undergoing dark treatments is the stimulation of a germination response by the weak red or green light. The use of a green safe light is common practice in germination studies comparing the response of seeds to light exposure and darkness (Baskin and Baskin, 1976; Ikuma and Thimann, 1963). A study by Butler et al. (1964) showed that the major absorption bands of light in seeds were red (660nm) and far-red (730nm), with some minor absorption in the blue (450nm) and near U.V. wavelengths. Very little photoconversion of phytochrome was recorded within the green band of visible light (wavelengths of ~460nm to ~580nm). This would suggest that the use of green light is unlikely to stimulate a germination response in seeds. Some authors however have questioned the use of green light when inspecting ‘dark controls’ as it has been shown to stimulate germination. Baskin and Baskin (1979) showed that exposure of *Stellaria media* seeds to low intensity green light resulted in high percent germination. Valio et al. (1972) support these findings with green light showing a ‘surprising’ increase in germination response (43% - 57%) of *Bidens pilosa* seeds compared to dark controls (11% - 26%). In both studies, it was suggested that the seeds of these two species were highly sensitive to light. Baskin et al. (2006) suggest that stimulation of a germination response by green light is dependent on a particular species, the time of year (i.e. degree of after ripening) and the quality of light. As well as green light, red light has been shown to universally stimulate a germination response in seeds (Taylorson, 1972; Valio et al., 1972; Williams, 1983) and was therefore inappropriate for checking germination in darkness. The findings of previous research, coupled with the results of the study, suggest that marram grass seed is particularly sensitive to light and that the use of green and red safety lights to check the dark treatments may have resulted in the stimulation of a germination response.

This sensitivity to light may be a result of the random nature of burial and exposure in dune systems (Zhang and Maun, 1994) which make it advantageous for seeds to have a high sensitivity to light in order to react quickly to rapid changes in burial depth. This is supported by the findings of Woolley and Stoller (1978) who suggest that dormant seeds brought to the surface by cultivation, may receive light during the cultivation process or indirectly through the soil, resulting in germination. Dyer (1995) also suggests that agricultural practices such as tillage can expose seeds to light, breaking dormancy and facilitating germination. This is similar to the coastal environment, where the shifting sediment results in the uncovering of seeds to a level at which light can be received. The fact that marram grass seed showed some germination under both red and green lights suggests that it is highly sensitive to light and thus is able to exploit light as a germination cue in low exposures in a natural setting.

The case of high light sensitivity in marram grass seed is further supported by the findings of the dark red treatment. This experiment showed a very rapid rate of germination, higher than those seeds exposed to light. Several studies have been conducted investigating light penetration into different soil types under different physical states i.e. dry or moist (Tester and Morris, 1987). The increased rate of germination seen in seeds exposed to red light may reflect the findings of Bliss and Smith (1985). Their study aimed to determine whether the quality and quantity of light penetrating into certain soils was capable of inducing germination in seeds of several plant species. They found that in coarse sand, there was a rapid attenuation of shorter wavelengths accompanied by a relative transparency to longer wavelengths. They concluded that seeds of some species responded to small amounts of longer wavelength light below-soil. In marram grass seed this may also be the case, with a much greater germination response seen in seeds exposed only to red light.

Alternatively the seeds may have reacted to the light in which they were handled in prior to being placed in the light-proof bags. When the seeds were being selected from the pool of Oreti Beach seed and prepared for germination, they were exposed to both natural and artificial light, which may have been enough to stimulate a germination response. The findings of Wesson and Wareing (1969b) showed that even very short bursts of exposure to high intensity white light (in their study, 90 seconds) was sufficient for the germination of a large proportion of weed seeds in agricultural fields. Marram grass seeds' high sensitivity to light may be such that even these short exposures to artificial and natural light during preparation for the dark treatments was enough to facilitate germination.

3.6.3 The effects of burial on germination

The results of the emergence from burial experiment have shown that marram grass seed is unable to emerge from any depths greater than 5 cm. The level of emergence was also found to reduce dramatically between 0.5 cm and 5 cm of burial, although the rate at which emergence occurred was approximately the same. This finding reflected that of Huang et al. (2004) who found that among the different sizes of caryopses of the perennial grass *Leymus racemosus*, maximum seedling emergence occurred at 0 – 0.5 cm depth. Likewise in a study conducted by van der Meijden and van der Waals-Kooi (1979), maximum germination of *Senecio jacobaea* seeds was observed in burial depths of 1 mm, with no seedlings emerging in the 8mm or 16mm burial treatments. In marram grass seed, the lack of emergence from burial depths of greater than 5 cm suggests that the process of burial induces dormancy, which may potentially be explained by three phenomena: 1) increasing burial depth reduces the ability of light to penetrate the soil, removing the light stimulus required for germination to occur; 2) that gaseous inhibitors produced by the seeds' metabolism following burial may result in the inhibition of germination; and/or 3) that the compaction of sediment around marram grass seed during burial may prevent the penetration of the radicle through the glumes thereby inhibiting germination and emergence.

Identifying the exact mechanisms behind the induction of dormancy in marram grass seed is beyond the scope of this study, however the results of the light and dark experiments may have some explanatory value when considering dormancy. When seeds become buried in increasingly deeper layers of substrate, the amount of light that reaches the seeds may be dramatically reduced, thereby inhibiting germination (van der Meijden and van der Waals-Kooi, 1979; Woolley and Stoller, 1978). Tester and Morris (1987) in their review of studies relating to the penetration of light into soil found that generally, light rarely penetrated deeper than 4 – 5 mm depth in any soil. The findings of section 3.5.3 suggest that marram grass seed is strongly light sensitive in terms of germination and as a consequence, those seeds buried in depths greater than 5 cm, and even at depths between 0.5 cm and 5 cm, may not receive the necessary level of light required for germination to occur. Therefore, burial acts as a mechanism for depriving seeds of light below a certain depth, potentially resulting in the induction of dormancy.

Alternatively to decreasing light penetration through soil, Wesson and Wareing (1969a) present a second theory for understanding the processes that inhibit germination of buried seed. In their study of light sensitivity in seeds before and after burial, one species in particular, *Plantago lanceolata*, showed a relationship between 0 – 2 cm of burial and the inhibition of germination. The study suggested that germination may be related not only to the penetration of light through the substrate, but also its water content, with germination being inhibited in water contents in excess of 80%. It was suggested that a combination of burial depth and water content restricts aeration of soil which in some way inhibits seed germination. The addition of compressed air to potted samples showed that, once the soil was aerated, seeds germinated. Two possible effects of aeration were proposed: 1) that aeration increases the levels of a promotive substance, assumed to be oxygen; or 2) that aeration removes an inhibitory substance, assumed to be carbon dioxide, following Kidd’s (1914) carbon dioxide-narcosis theory. Subsequent testing of these two theories showed that oxygen was not a limiting factor in germination and that another gaseous inhibitor, besides carbon dioxide, was the cause of inhibition. It was deemed that an inhibitor as a product of the seeds’ metabolism was the cause for this dormancy (Wesson and Wareing, 1969a). Although this phenomenon has not been identified in marram grass seed, this may potentially play a role in the inhibition of germination and further research is required.

During excavation, it was initially thought that recovered seeds had one of two different fates: 1) germinated and subsequently emerged; or 2) not germinated. Viability testing however indicated a third fate, where seeds had germinated but the radicle did not penetrate the glumes, for seeds buried at 10 cm and 15 cm. This observation may have been caused by two phenomena. Firstly, burial may inhibit germination by preventing penetration of the radicle through the glumes as a result of the pressure placed on the seed by the covering sediment. A search of the literature was unable to find studies that support this idea, however future research may indicate whether or not this is a potential mechanism for preventing seedling emergence in marram grass. Alternatively seeds may have begun to germinate after excavation and exposure to light during preparation for viability treatments. Unfortunately, the exact cause for this third fate could not be determined.

Although the length of burial during the current investigation was relatively short (42 days), the results of the germinability and percent viability tests suggest that marram grass seeds develop at least a temporary dormancy during storage in sandy substrates. Testing of the recovered seed for germinability showed a high percentage of germination (79.5% to 90%). Tetrazolium chloride staining of subsequently ungerminated seeds also indicated potential viability in the seeds recovered from all of the burial depths except the 20 cm treatment. These results indicate that, after burial, only a small proportion of seeds lose their viability whilst a greater proportion exists in a state of induced dormancy. This ability of marram grass seed to be buried yet remain viable supports the idea that marram grass can form seed banks in natural environments (Chapter 5).

3.6.4 Low seed recovery from excavations

In section 3.5.4 a lower than expected rate of seed recovery was experienced during excavation of the burial treatments. This low rate of recovery may have been a result of the excavation method used or human error. During the excavation process much of the sediment was still saturated by the watering treatment it had received over the 42 day period. This resulted in a sand colouration similar to that of the seeds that were being recovered, making it difficult to differentiate and collect all of the tested seeds. This may have been overcome by a drying process similar to that described in Chapter 5 (section 5.3.2), although this would have resulted in the inability to identify the depth from which seeds were collected. After conducting the excavation process however, no seeds were retrieved below the netting layer that marked the base level of burial. Although this may have been a result of human error, the findings suggest that sieving may have provided a greater recovery rate of seeds without compromising the quality of the data collection. Despite the low recovery rates of seeds ranging between 41.3% and 80% however, there were sufficient sample sizes to test germination and viability of buried marram grass seed.

3.7 Chapter summary

The germination of seeds requires optimal temperatures, availability of oxygen, adequate soil moisture and light among other factors. In the coastal environment, sparse vegetation cover, high soil porosity and low organic matter combine to make microenvironmental conditions particularly hostile to seed germination. However, the constant shifting of substrate often leads to the burial of dispersed seed, ameliorating these harsh growing conditions. Although germination conditions may become more suitable, burial at depths greater than light can penetrate, can lead to the onset of dormancy in seed. Therefore understanding the interactions between burial and the effects of light and darkness on marram grass seed is important in developing an understanding of the dispersal and invasion process in marram grass.

Before the effects of light versus darkness and burial on germination could be investigated, the percent germinability and viability of the seed collected from Oreti Beach was tested. This provided an indication of the background rate of germination that could be expected without these added factors. Percent germinability was tested using three different methods of germination, with the removal of all outer seed structures showing the greatest percent germinability (94%). Percent viability testing involved the use of the tetrazolium chloride to chemically test seed viability. This produced a much lower estimate of seed viability (58%) compared to germinability however this finding was similar to that of Pope (2005) who used the same method.

Testing of the effects of light versus darkness on germination in marram grass seed showed that seed is highly sensitive to light. This high sensitivity to light was attributed to two scenarios: 1) a strong, innate sensitivity to even weak green and red light possessed by marram grass seed; and/or 2) that seeds may have reacted to artificial and natural light exposure during preparation for germination in the dark. Although determining the exact mechanism was beyond the scope of the study to identify, this suggests that marram grass seed is well adapted to the constantly shifting substrate in the coastal environment which may result in rapid changes in burial.

Marram grass seeds were shown to emerge from between 0.5 cm – 5 cm of burial, with no emergence observed in depths of 10 cm, 15 cm or 20 cm. Percent emergence was also far greater under 0.5 cm of burial (29.33%) compared to 5 cm of burial (4%). Subsequent germinability and seed viability testing has shown that although many seeds did not germinate and emerge, a large percentage remained viable during the 42 day burial period. Three potential causes of germination inhibition at depths greater than 5 cm were presented: 1) that seedling emergence was inhibited by the lack of a light stimulus; 2) that an inhibitor from the seeds' metabolism may have enforced dormancy in seeds; and/or 3) that compaction by the sediment surrounding the seed prevented the penetration of the radicle through the glumes. When considering the results of the light and dark aspect of the investigation it would appear that the prevention of light penetration through the soil may play the biggest role in inhibiting germination following burial. The inhibition of germination and induction of dormancy associated with burial supports the findings of Chapter 5 and suggest that marram grass seed is capable of forming a viable seed bank.

Chapter 4

Seedling distribution

4.1 Overview

The quantification of seed crop size and the identification of factors affecting germination further understanding of the invasion process by marram grass seed. In conjunction with this, the analysis of seedling distribution within the central dune system at Mason Bay may provide useful information relating to those dune environments that are likely to facilitate emergence and establishment in seedlings and thus contribute to the development of strategies for marram grass control.

Observational evidence from control operations at Mason Bay, suggests that marram grass may invade into the central dune system via seed. Figure 6.3 highlights the distribution of seedlings in the central dune system of Mason Bay relatively far from the closest flowering populations of marram grass, which are located in the foredune complex and along the trailing arms of the parabolic dunes. Analysing seedling distribution works towards Objective one by furthering understanding of downwind invasion by marram grass seed and obtaining some estimate of the distance over which seed may travel. Therefore, Chapter 4 aims to analyse seedling distribution patterns in the central dune system of Mason Bay which can be used to inform both the development of a conceptual invasion model and future management recommendations.

4.1.1 The importance of microsites in seedling establishment

The location where a seed finally settles and germinates is affected significantly by variations in soil microtopography, which may provide ‘safe sites’ for seed germination at different times and places (Chambers and MacMahon, 1994; Harper *et al.*, 1961). Microtopography in this case refers to crevices, surface depressions, gravel/stones and other plant species (Franks, 2003; Harper *et al.*, 1965; Winkel *et al.*, 1991). Small-scale variations in microtopography of the surface can generate an array of microsites potentially available for occupation by propagules, provided a species sets sufficient seed to discover these safe sites (Harper *et al.*, 1961; Peart, 1984).

It is generally accepted that safe sites benefit seeds the most through the modification of seed-water relationships and the protection of seeds from desiccation (Fowler, 1986; Harper *et al.*, 1965). Collis-George and Sands (1959) suggested that the ideal seedbed is one where the seed is surrounded by firmly packed soil particles to increase the conductivity of water from soil to seed. Sheldon (1974) showed that microsite treatments creating high humidity tended to have greater germination and establishment compared to bare surfaces, due to the quicker accumulation of water for germination. Evans and Young (1972) in another study of microsite requirements of annuals in western American rangelands, found a 100 times increase in germination of Downy Brome (*Bromus tectorum L.*) seeds when placed in small pits dug into the ground. It was suggested that these depressed sites retained soil moisture at the surface layer for longer and provide more favourable atmospheric moisture and temperature regimes compared to bare flat surfaces. In the coastal dune environment, it would therefore be expected that those surface features that ameliorate the extremes of soil moisture and temperature commonly experienced at the dune surface, would be most ideal for the germination of marram grass seed.

Seedlings face many hazards during establishment and colonisation of new areas, and in coastal dune environments, the risks are especially high due to spatial and temporal variability of the substrate (Fenner, 1987; Maun, 1994). Limiting factors to establishment may include shortages in water or nutrients, salt spray and sand burial or erosion (Ishikawa, *et al.*, 1995; Maun, 1994, 2009). De Jong and Klinkhamer (1988) found that in a sand-dune area at Meijendel, Netherlands, seedling survival in two biennials was positively correlated with the water content in the top 10 cm of soil. The seedlings of both *Ammophila arenaria* and *A. breviligulata* also showed greater emergence in wet dune environments such as wet slacks, the lee of dune ridges and on the margins of inner dune swales in Wales and North America respectively (Huiskes, 1977; Laing, 1958). This has largely been attributed to the prevention of desiccation in seedlings and again highlights the importance of water availability in the dune environment. The soil moisture content of different dune environments must therefore be considered as a key factor when analysing patterns of marram grass seedling distribution at Mason Bay.

From the existing literature on the importance of microsites to seed germination, it is apparent that some dune environments may be more beneficial to the germination and establishment of seeds/seedlings than others. Deflation surfaces are those areas in the dune environment where the sand surface has been eroded to the seasonal water table or a coarse, less mobile layer i.e. stones (Carter *et al.*, 1990). Due to their proximity to the water table, these surfaces may provide the ideal soil moisture conditions necessary to act as potential safe sites and will therefore be the focus of this chapter. In the central dune system of Mason Bay, three types of deflation surfaces were identified: 1) stonefields; 2) wet depressions; and 3) wet communities. Stonefields consisted of low-lying, damp, deflation areas covered in small stones. It is thought that these stones afford some shelter for seeds from desiccation as well as facilitating burial of seed due to an increase in surface roughness (Chambers and MacMahon, 1994). Wet depressions and wet communities were similar in that they both were low-lying deflation zones with the water table visibly close to the surface; however they differed with respect to vegetation. Wet depressions tended to have little to no vegetation besides small marram grass or *Poa billarderei* seedlings, while the wet communities had a more consistent covering of vegetation and a more complex vegetative community. The wet sand of both environments may provide favourable microsites for the establishment of seedlings by reducing desiccation and the risk of catastrophic micro-erosion following seed settlement (Maun, 2009). This chapter therefore aims to explore the relationship between seedling distribution and the different dune environments at Mason Bay.

4.2 Method

4.2.1 Analysis of seedling distribution

Data collection was completed in a two-part process using both primary GPS data collected in the field with a Garmin 76CS GPS unit and secondary GPS data collected from previous research between 2006 and 2009. This data was analysed using ArcMap version 9.3.1. The base map of Mason Bay used during this investigation was downloaded from Google Earth (taken in 2009) and georeferenced using six ground control points evenly spaced around the central dune system (Figure 4.1) The ground control points were selected from a set of GPS points collected in 2006 of features that were visible in a set of aerial photographs that were also flown in 2006. A preference was shown for permanent man-made structures, such as the historic homestead and public hut, as ground control points because these were unlikely to change over a significant time period. Unfortunately, due to the remote nature of Mason Bay, few permanent structures have been built and therefore less permanent features such as vegetated sand dunes also had to be used. These less permanent features from the 2006 aerial photographs were matched with the same feature shown on the 2009 Google Earth image. The resultant Root Mean Square (RMS) error of 6.66 was deemed to be satisfactory for the requirements of this investigation.

4.2.2 Primary data collection

Before analysis of seedling distribution patterns could commence, the boundaries of the three types of deflation surfaces had to be demarcated. This was achieved through the collection of primary GPS data from the central dune system of Mason Bay during January 2010. All instances of these environments were circumnavigated using a Garmin 76CS GPS unit and marked with an appropriate label i.e. ‘Stonefield 1’. The GPS unit was switched off between deflation surfaces which resulted in a ‘breadcrumb’ walking trail around each of the areas of interest. These were then downloaded into ArcMap and drawn into a polyline shapefile (Figure 4.2). During analysis of the deflation surface polygon layer, it was thought the area of the stonefield below Big Sandhill, marked with an ‘*’ on Figure 4.2, had already been collected during a previous study. Unfortunately this data could not be located and the stonefield was subsequently drawn by sight using the ‘editor’ tool in ArcMap.

Figure 4.1: The central dune system of Mason Bay with the six ground control points depicted.

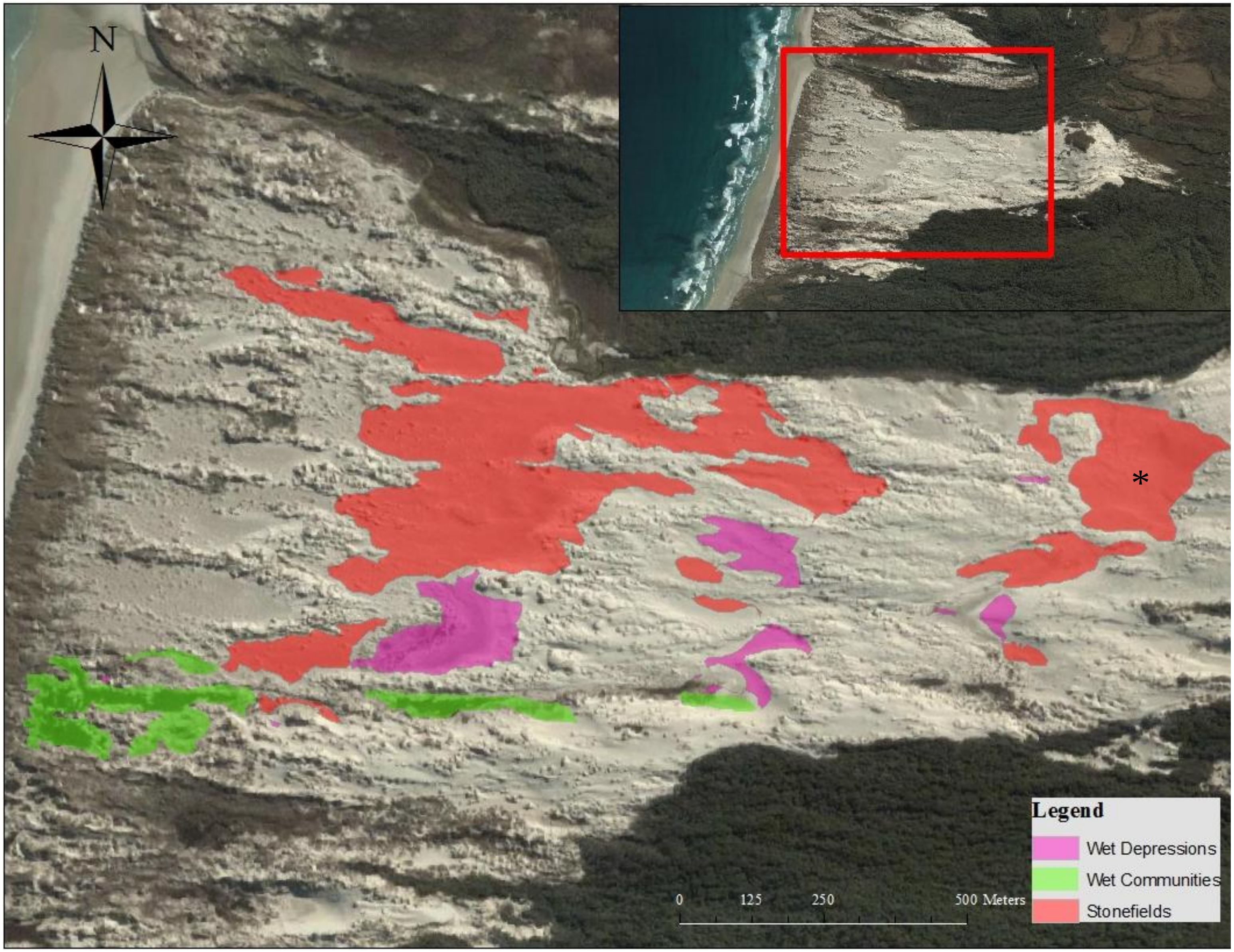

Figure 4.2: A map depicting the deflation surfaces in the central dune system of Mason Bay. * = The stonefield polygon drawn by sight.

4.2.3 Secondary data collection

The secondary seedling data used in this study was collected in January 2005, April and November 2006, October 2007 and June 2009, as part of the marram grass eradication operation that has been ongoing since 1998 in Stewart Island (Hilton and Konlechner, 2010). During these operations, volunteers and DOC rangers collected GPS data points of all seedlings that had either been manually removed or located and left in place. This procedure provided the study with an ideal dataset for elucidating the relationship between seedling distribution and the deflation surfaces in the central dune system of Mason Bay.

The separate seedling layers were merged using the 'merge' tool in the ArcMap toolbox. This created a single 'seedling' layer, with a total of 3,623 individual points, denoting seedlings, which could be compared against the three deflation surfaces. During the analysis of the secondary seedling data, it was acknowledged that the seedling data obtained from the seaward-most stonefield was not as reliable due to inconsistencies in survey procedures between years (Figure 4.4). Therefore the more reliable data from the central dune region was used, which is highlighted in Figure 4.3 by a red rectangle. To determine the number of seedlings that fell within the deflation surface polygons the 'search by location' function was used. This selection included all those data points that 'intersected' (or geometrically shared a common part with the source feature) each of the deflation surfaces. The total number of seedlings in the 'seedlings' layer and the total number of seedlings contained within each of the deflation surfaces were determined by looking up the attribute table of each layer. Finally the total area occupied by each of the deflation surfaces was calculated using the 'calculate geometry' function in ArcMap.

The analysis of seedling distribution against deflation surfaces was also carried out using the less reliable data in order to include the seedlings that were found in the large seaward stonefield. For this investigation, the same method as the one for the more reliable data was used, however the study area was extended to include the large stonefield as well as the wet community and wet depression further seaward of the original study area (Figure 4.4). The reduced reliability of this data is highlighted by the lack of points in the north-west corner of the study area, which may have been a result of inconsistent survey procedures. It was however deemed important to analyse this data because of the numerous seedling data points located in the wet depression, the edge of the wet communities and the stonefields which may change the proportion of seedlings found within each of the deflation surfaces compared to outside these areas.

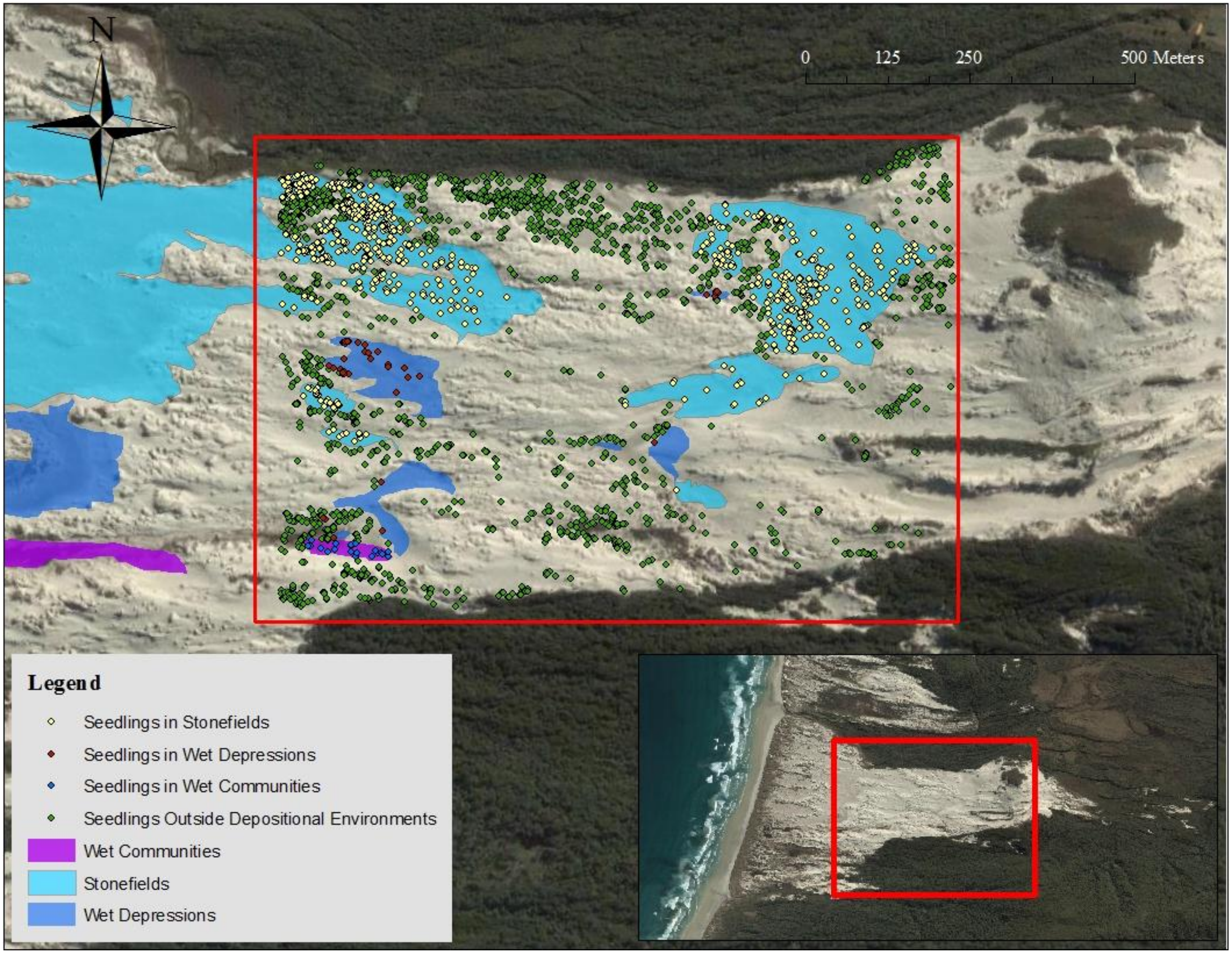

Figure 4.3: The analysis of the relationship between seedling distribution and deflation surfaces in the central dune system of Mason Bay. The data used for this analysis was considered to be more reliable and the area under investigation is highlighted by the red rectangle.

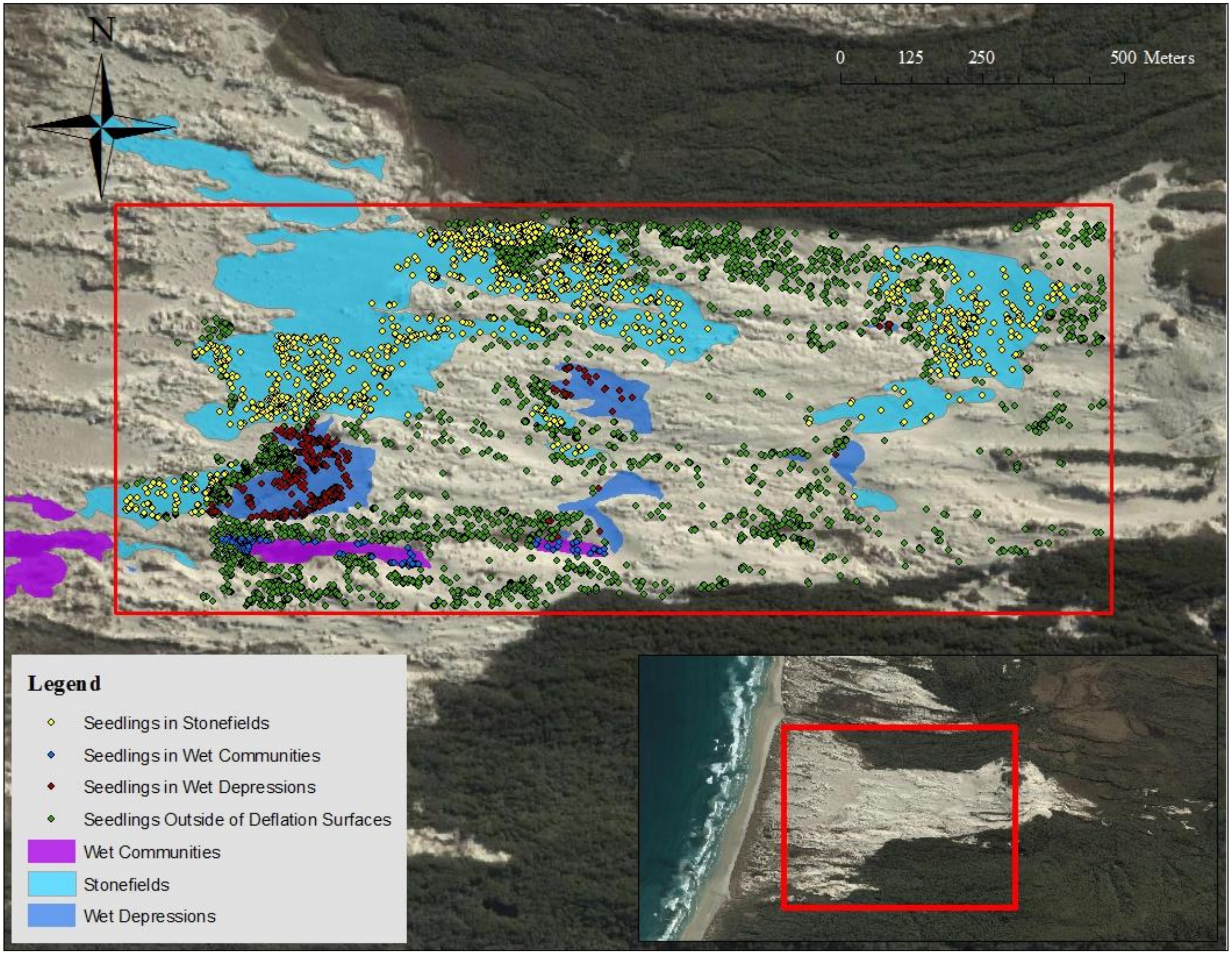

Figure 4.4: The analysis of the relationship between seedling distribution and deflation surfaces in the central dune system of Mason Bay. The data used for this analysis was considered to be less reliable and the area under investigation is highlighted by the red rectangle.

4.3 Results

4.3.1 Analysis of seedling distribution

In this section, the findings of the more reliable dataset will be presented first, followed by the less reliable dataset. The 'seedling' layer contained 3,623 data points (or seedlings) which were collected between January 2005 and June 2009. Of the 3,623 data points, 1,150 were contained within the three deflation surfaces, while 2,473 were found outside the deflation surfaces. The proportion of total seedlings found within the three deflation surfaces was 31.74% compared to 68.26% for those seedlings found outside of the three deflation surfaces (Table 4.1).

Table 4.1: A summary of the total number of seedlings (n = 3,623) and where they were located during the analysis of seedling distribution. The proportion of seedlings both within and outside of the deflation surface boundaries is also included.

Total seedlings	3,623
Total seedlings within a deflation surface	1,150
Total seedlings outside of a deflation surface	2,473
Proportion of total seedlings found within deflation surfaces	31.74%
Proportion of total seedlings found outside of deflation surfaces	68.26%

An analysis was also conducted into the distribution of seedlings between each of the deflation surfaces. In the stonefields, 1,086 seedlings or 94.43% of the total seedlings were contained within the boundaries of the stonefields (Table 4.2). Both the wet communities and wet depressions contained relatively few seedlings with 22 (1.91%) and 42 respectively (3.65%). It should however be noted, that the total area (m^2) of the deflation surfaces varied greatly and therefore an analysis of the number of seedlings per 100 m^2 was also calculated for comparison. The stonefield covered a total area of 246,534.48 m^2, compared to the wet communities and depressions which covered areas of 2,814.86 m^2 and 22,973.71 m^2 respectively. In the stonefield, a density of 0.44 seedlings per 100 m^2 was calculated compared to 0.78 and 0.18 seedlings per 100 m^2 in the wet communities and wet depressions respectively.

Table 4.2: A summary of the total area of each of the three deflation surfaces and the total number of seedlings (n = 1,150) contained within their boundaries. The percentage of total seedlings and seedling density are also included.

Deflation surface	Total area (m^2)	Number of seedlings	Percentage of total seedlings	Seedlings per 100 m^2
Stonefield	246,534.48	1,086	94.43%	0.44
Wet community	2,814.86	22	1.91%	0.78
Wet depression	22,973.71	42	3.65%	0.18

In the less reliable dataset, the 'seedling' layer contained a total of 7,667 data points (or seedlings). Of the 7,667 seedlings, 2,980 were contained within deflation surfaces and 4,687 were found outside deflation surfaces. The proportion of seedlings found within deflation surfaces was 38.87% compared to 61.13% outside. This data is summarised in Table 4.3.

Table 4.3: A summary of the total number of seedlings (n = 7,667) and where they were located during the analysis of seedling distribution. The proportion of seedlings both within and outside of the deflation surface boundaries is also included.

Total seedlings	7,667
Total seedlings within a deflation surface	2,980
Total seedlings outside of a deflation surface	4,687
Proportion of total seedlings found within deflation surfaces	38.87%
Proportion of total seedlings found outside of deflation surfaces	61.13%

The distribution of seedlings among the deflation surfaces in the less reliable dataset showed a similar pattern to that seen in the more reliable dataset. A key finding however, was that the seedlings showed a more even distribution across all three deflation surfaces, where the proportion of seedlings in the stonefields, wet communities and wet depressions were 67.89%, 8.12% and 23.99% respectively (Table 4.4). The density of seedlings per 100 m^2 differed compared to the reliable dataset with the stonefields showing the lowest density (0.77 seedlings per 100 m^2). The wet community had the lowest area but had the greatest density (1.84 seedlings per 100 m^2) and the wet depressions increased in density from 0.18 to 1.4 seedlings per 100 m^2 from the more reliable to less reliable datasets.

Table 4.4: A summary of the total area of each of the three deflation surfaces and the total number of seedlings (n = 2,980) contained within their boundaries. The percentage of total seedlings and seedling density are also included.

Deflation surface	**Total area (m^2)**	**Number of seedlings**	**Percentage of total seedlings**	**Seedlings per 100 m^2**
Stonefield	263,253.85	2,023	67.89%	0.77
Wet community	13,181.23	242	8.12%	1.84
Wet depression	50,991.78	715	23.99%	1.4

4.4 Discussion

4.4.1 The relationship between seedling distribution and dune environment

Analysis of seedling distribution in the central dune region of Mason Bay suggests that seeds are not primarily dependent on naturally moist conditions or surface obstructions such as stones or vegetation in order to germinate and establish. This is evidenced by the greater proportion of seedlings found outside compared to within the deflation surfaces (Tables 4.1 and 4.3). Generally the available literature suggests that marram grass seedlings emerge, and a small fraction will establish, in predominantly wet environments such as the dune slack in the lee of a dune ridge (Huiskes, 1977). At Mason Bay, this does not appear to wholly explain the process of dispersal and establishment of marram grass seed/seedlings.

Further exploration of the patterns of seedling distribution between the three deflation surfaces showed that the stonefields contained the greatest number of seedlings. However, the stonefields also covered the greatest area and as a result had the smallest density of seedlings. The wet community on the other hand contained the greatest density of seedlings yet covered the smallest area. The wet depressions contained differing densities of seedlings depending on whether the more or less reliable data was used however the less reliable data also included one large wet depression which contained many seedlings. This analysis suggests that certain environments are more effective at trapping marram grass seed and facilitating establishment of seedlings compared to others. The processes that may facilitate germination and establishment of seeds/seedlings in each of the dune environments (both deflation surfaces and other dune environments) are discussed in the following section.

4.4.2 Germination and establishment in stonefields

Following the findings of studies investigating favourable microsites, it was originally thought that deflation surfaces such as stonefields, wet depressions and wet communities would provide ideal conditions for the germination and establishment of marram grass seeds/seedlings. In stonefields, seeds were expected to be caught by obstructions on the sands' surface such as rocks and established tufts of Pingao and *Poa billardierei* due to increases in surface-roughness. These abiotic and biotic obstructions often act as natural seed traps and serve as accumulation sites due to the generation of eddies or wind shadows which trap entrained seed in both water and wind (Chambers and MacMahon, 1994) (Figure 4.5). As well as acting as sites for the accumulation of seed, these abundant surface obstructions may also act as safe sites to ameliorate extremes of moisture and temperature in the dune environment, enabling germination (Fowler, 1986; Winkel *et al.*, 1991). Harper *et al.* (1965) found that one of the key benefits of such microsites is the beneficial modification of seed-water relationships which facilitates germination. Winkel *et al.* (1991) suggest that one of the most important characteristics of a microsite is the association with high humidity and soil moisture.

Figure 4.5: Marram grass emerging through and displacing an established pingao individual.

4.4.3 Germination and establishment in wet depressions

From the available literature, it would be expected that seeds preferentially germinate and establish in wet depressions as opposed to other dune environments. Marram grass seedlings from around the world have been observed to emerge primarily in wet slacks, the lee of dune ridges and on the margins of inner dune swales (Huiskes, 1977; Laing, 1958). In southern New Zealand however, this does not appear to be the case and suggests other factors are involved in determining seedling emergence. The wet depressions in other dune environments are subject to a relative degree of shelter behind dune ridges and vegetation which may ameliorate the harsh dune conditions (Huiskes, 1977). At Mason Bay, wet depressions are often in very exposed locations and seedlings may therefore experience very harsh growing conditions. Wet depressions are also located in areas experiencing net erosion, as evidenced by the erosion of sand to the seasonal water table. This net erosion and the lack of any surface obstructions may result in very little burial in these environments. This can lead to desiccation of marram grass seeds and seedlings, the failure of marram grass seed to settle in these environments and/or the lack of fresh sand input necessary for marram grass growth. All these factors may contribute to a reduction in seedling establishment on these deflation surfaces.

4.4.4 Germination and establishment in wet communities

In a wet community, the moist conditions coupled with a potential nurse plant effect from already established plants may provide marram grass seeds with microsites that facilitate germination and establishment. The “nurse effect syndrome” was coined by Niering *et al.* (1963) and describes the phenomenon of enhanced seedling establishment in the vicinity of adult plants that ameliorate extreme environmental conditions (Padilla and Pugnaire, 2006). In the central dune system of Mason Bay, these established plant species may provide benefits such as increased levels of soil fertility, soil moisture and protection from the desiccating effects of the wind and the sun (Franco- Pizaña *et al.*, 1996; Pugnaire *et al.*, 1996; Shreve, 1931). This would theoretically work to improve the chances of establishment in marram grass seedlings and may increase the rate of settlement by providing a surface roughness similar to the stonefield.

In this study these factors may have played a small role in facilitating germination and establishment in marram grass seed/seedlings. This is evidenced by the greater density of seedlings per 100 m^2 compared to the other deflation surfaces. However, marram grass germination and establishment in these environments was often documented on the edges, away from the densest patches of vegetation suggesting that these plant species may in fact decrease the chance of marram grass seed to emerge and establish. In its role as a dune pioneer species, marram grass is well adapted to conditions of low nutrient availability, with extensive horizontal and vertical root networks (Pavlik, 1983). However in areas where other species have become established, marram grass may not possess the ability to compete for resources, reducing the ability of seedlings to germinate and establish in a wet community (Marshall, 1965). Combined with this potential competition, the wet communities occupied a relatively small area compared to the other dune environments so do not make a large contribution to the total pool of seedlings.

4.4.5 Germination and establishment in other dune environments

Although the previous discussion has addressed the differences in seedling distribution between each of the three deflation surfaces, the key finding, that marram grass seedlings were more abundantly distributed outside deflation surfaces, has not been discussed. No explanation for this phenomenon is presented in the current literature, which is most likely due to the fact that seedlings found in other studies have all been located in wet slacks, the lee of dune ridges and on the margins of inner dune swales (Huiskes, 1977; Laing, 1958). Contrary to these relatively sheltered microsites, in the sandsheet environments disturbance by sand acts as a strong selective force that primarily drives species composition in sand dune communities (Forey *et al.*, 2008). At Mason Bay, three hypotheses may explain the seedling distribution found during this investigation: 1) seeds located outside of deflation surfaces have a greater chance of burial; 2) the sandsheet environments are more extensive compared to deflation surfaces; and 3) the rainfall regime at Mason Bay makes conditions mesic enough to nullify any advantages that deflation surfaces possess over sandsheet environments.

Sedimentation dynamics may be a key factor behind the favourable distribution of seedlings in the sandsheet environments compared to the deflation surfaces. As mentioned previously, the deflation surfaces are in a state of net erosion which may result in death by desiccation, the failure of seeds to germinate and the lack of fresh sand to stimulate growth. In contrast, the sandsheet environments are not in a state of net erosion and therefore seeds settling here may quickly become buried, ameliorating the harsh dune conditions. Any seedlings establishing in the sandsheet environments may also receive adequate supplies of fresh sand stimulating growth. Marram grass seeds also possess sharply pointed calluses and hygroscopically active awns which are thought to facilitate burial (Huiskes, 1979; Mott, 1978). These awns help to anchor seeds into cracks, crevices and under surface obstructions, increasing contact between the soil and the diaspore thereby increasing survival (Peart, 1979; Pope, 2005). Peart (1979) also demonstrated that de-awning seeds resulted in a decrease in movement to suitable microsites, poorer germination and decreased establishment of seedlings. In a drier sand environment, such as the sandsheets, the less compacted nature of the sand as well as the constantly shifting substrate may facilitate rapid burial. Following burial, the harsh conditions of the sand dune environment are ameliorated, increasing the likelihood of successful germination and establishment in marram grass seed (Maun, 1998). Therefore more rapid burial in the sandsheet environment may also play a key role in facilitating germination and establishment in marram grass seedlings.

Similar to the stonefields, the bias in distribution of seedlings towards the sandsheets may be due to their greater extent in the central dune system at Mason Bay compared to the deflation surfaces. Unfortunately the actual area of sandsheet contained within the study area could not be ascertained however Figures 4.3 and 4.4 suggest that the sandsheets occupied a larger area compared to the deflation surfaces. This increases the chance that seeds will emerge and establish in these environments over the deflation surfaces and may explain the more abundant distribution of seedlings found in the sandsheets.

The idea that establishing seedlings would show a preference for deflation surfaces was supported mainly by studies investigating the benefits of safe sites (Harper *et al.*, 1965). The key benefit was the improvement of seed-water relationships which ameliorated the harsh growing conditions associated with the coastal dune environment (Collis-George and Sands, 1959; Evans and Young, 1972; Fowler, 1986). At Mason Bay however, the annual rainfall is approximately 1,324mm, placing it in the ‘wet winter temperate zone’ (van der Maarel, 1993). Widemann and Pickart (2008) suggest that this ‘temperate’ classification implies that the dune environment experiences neither extremes in temperature nor very low levels of precipitation. The relatively mesic environment at Mason Bay may therefore nullify any advantages that the safe sites of the deflation surfaces possessed over the sandsheets for establishment. Therefore the combination of a mesic climate and supply of fresh sand coupled with a potentially greater overall area may be behind the greater distribution of seedlings in the sandsheets compared to the deflation surfaces.

4.5 Chapter summary

The analysis of seedling distribution in marram grass compliments previous research conducted in this study that estimated seed crop size in different depositional environments at Mason Bay (Chapter 2) as well as those factors that may affect germination in marram grass seed (Chapter 3).

Following dispersal, a seed must settle in an ideal environment for germination and establishment to occur. These are termed ‘safe sites’ and may form naturally as crevices, surface depressions, gravel/stones or other plant species. From the current literature it would appear that the greatest benefit offered by these microsites is the modification and improvement of seed-water relationships, with water being a vital factor in germination. Understanding which factors aid in germination and establishment and which dune environments seedlings are likely to establish in will provide valuable information for future marram grass control operations and therefore was a key focus of this chapter.

The analysis of seedling distribution at Mason Bay was conducted with a combination of primary and secondary data. The results suggest that a much greater number of seedlings are distributed outside of the deflation surfaces compared to inside. Within the three different deflation surfaces, stonefields contained the greatest number of seedlings compared to the wet depressions and communities. Further analysis showed that the wet communities had a greater density of seedlings per 100 m^2, while covering a much smaller area. The less reliable data also showed a much greater density of seedlings per 100 m^2 in wet depressions compared to stonefields.

Within the deflation surfaces, seedling distribution was expected to be greater due to the abundance of stones and plants that may provide safe sites for the germination of seed. In wet depressions and communities, a greater distribution was also expected due to the increased level of moisture in these environments and the amelioration of temperature extremes by established plants. However, it was apparent from the study that other factors play a key role in determining seedling distribution at Mason Bay. A reason suggested for this trend was that the erosional nature of the deflation surfaces deprived seeds of fresh sand and potentially exposed them to desiccation by wind and insolation. In the sandsheet environment, three other factors were suggested which may have resulted in the seedling distribution patterns found by this study: 1) seeds outside of deflation surfaces have a greater chance of burial; 2) the sandsheet environments are more extensive compared to deflation surfaces; and 3) the rainfall regime at Mason Bay makes conditions mesic enough to nullify any advantages that deflation surfaces possess over sandsheet environments. It is most likely a combination of all three factors that dictate the distribution of seedlings observed during the analysis in this chapter.

Although the mechanisms behind the observed patterns of seedling distribution are not entirely clear, this analysis has provided valuable information for future control operations. Identifying areas that are more likely to facilitate seedling establishment allows for the strategic targeting of control operations. The findings of this chapter also suggest that, in southern New Zealand, patterns of seedling distribution differ from those recorded in the current literature. Finally, this analysis has been used to inform the development of a conceptual model of invasion which will be presented in Chapter 6.

Chapter 5

Seed bank longevity

5.1 Overview

An understanding of the longevity of the seed bank is a key component for any invasive weed control strategy because this represents a primary source from which re-invasion can occur. In marram grass, this aspect of seed ecology has received little attention as it has largely been regarded as being less important to its general ecology (Huiskes, 1979; Hertling and Lubke, 1999; Krajnyk and Maun, 1982; Maun, 1984, but for an exception see Huiskes, 1977). As a result, there have been few studies focusing on marram grass seed bank longevity; despite observations that marram grass seed may possess some form of dormancy (Konlechner and Hilton, 2009). This therefore highlights a key gap in the understanding of marram grass seed ecology.

The second objective of this study is to determine if marram grass forms viable seed banks in southern New Zealand. The three research questions within this objective are:

1. Does marram grass form viable seed banks in southern New Zealand?
2. If so, how long does seed remain viable?
3. What proportion of seed remains viable?

This chapter therefore aims to investigate the nature and longevity of marram grass seed banks in two southern New Zealand dune systems, St Kilda Beach and Allan's Beach using two novel approaches to sampling the seed bank.

5.2 Seed bank formation in coastal environments

The seed bank has been defined as an aggregation of all un-germinated, viable seed, potentially capable of replacing adult plants on or in the soil and/or contained within the associated plant litter (Baker, 1989; Simpson *et al.*, 1989). The presence of a seed bank is often considered to be the primary source of infestation in subsequent growing seasons and is crucial to the maintenance of plant populations (Rao, 2000; van der Hagen *et al.*, 2008). In coastal environments, the continual re-distribution of sand by wind can lead to the burial of seeds under favourable conditions or the exposure of seeds to unfavourable conditions (Baskin and Baskin, 1998). The continually shifting substrate of this environment therefore makes the survival of seed particularly difficult and it is therefore conceivable that the formation of seed banks occurs in special circumstances or in a manner different to many other environments.

Planisek and Pippen (1984) in a study of beach, foredune, slacks and dune forest along the eastern shore of Lake Michigan concluded that there may be no persistent seed bank formation by any species present in this environment. Maun (2009) however suggests that, evolutionarily, seed banks are important in the dune complex because they provide insurance for species against the risks of frequent disturbance created by high velocity winds and erosive wave action. Thompson *et al.* (1998) supports Maun's view by demonstrating that increased habitat disturbance always selects for increased seed persistence. Zhang and Maun (1994) in their investigation of seed bank formation at Lakes Erie and Huron, South-western Ontario, Canada, found that buried seeds of seven dune species remained viable for at least 2.5 years; exhibiting the potential to form persistent seed banks. In the same study they also disputed Planisek and Pippen's (1984) findings because of three methodological errors: 1) inappropriate volume of soil and number of samples taken; 2) the depth of sample collection; and 3) disparities between sampling and local plant distribution and fruiting events.

In an invasive weed such as marram grass, the possession of a seed bank could potentially increase its ability to persist in a highly disturbed coastal dune environment. In southern New Zealand, Konlechner and Hilton (2009) identified the presence of a persistent marram grass seed bank at Doughboy Bay, Stewart Island. The spraying of marram grass at Doughboy Bay began in February 1999 and by 2003, regeneration of marram grass occurred only from seedlings. Since spraying operations ceased, there have been signs of germination from seed for ‘at least 9 years’ after the original spraying event (Figure 5.1) (Konlechner and Hilton, 2009). This provides impetus for a more comprehensive investigation into the nature of the marram grass seed bank in southern New Zealand. Understanding this phenomenon not only addresses the second objective of this study but also provides valuable information to land managers regarding the persistence of marram grass in an environment following initial control operations.

Figure 5.1: A marram grass seedling emerging from the gradually eroded foredune at Doughboy Bay.

5.3 Method

5.3.1 Study sites

The investigation of the marram grass seed bank took place at two dune systems within the Dunedin region, St Kilda Beach and Allan's Beach. This study was presented with a unique opportunity to investigate the nature and longevity of the marram grass seed bank due to the possession of two decades of aerial photographic and surveying data that records the temporal development of the two dune systems. This enabled two novel methods of seed bank investigation to be carried out that have not been conducted in any other study to date.

St Kilda Beach, Dunedin

St Kilda Beach (Figure 1.5), located approximately 5 km from the Dunedin city centre, was originally a belt of low lying sand dunes bounding tidal flats and swamps at the head of the Otago Harbour (Glassey *et al.*, 2003). This is vastly different to its present day appearance however, where human property is protected by two large artificially constructed dunes. It is the most seaward of these two dunes that provides an ideal site to sample the marram grass seed bank. The beach experiences wind from two predominant directions, south-west, which is generally the stronger of the two, and north-east, which is more persistent (Hodgson, 1966). The exposed nature of the St Kilda dune system, as well as the presence of flowering marram grass, leads to the accretion and progradation of the foredune. This creates ideal conditions for the formation of a seed bank, as any released seed is quickly buried and stored in cooler, drier conditions. A record of beach profile surveys exists for the seaward foredune dating back from August 2010 to March 1989 which allows for seed bank age to be correlated with depth (Figure 5.2). The combination of a lengthy dune profile record and the formation of a measurable seed bank therefore make St Kilda an ideal site for sampling the marram grass seed bank and investigating its longevity.

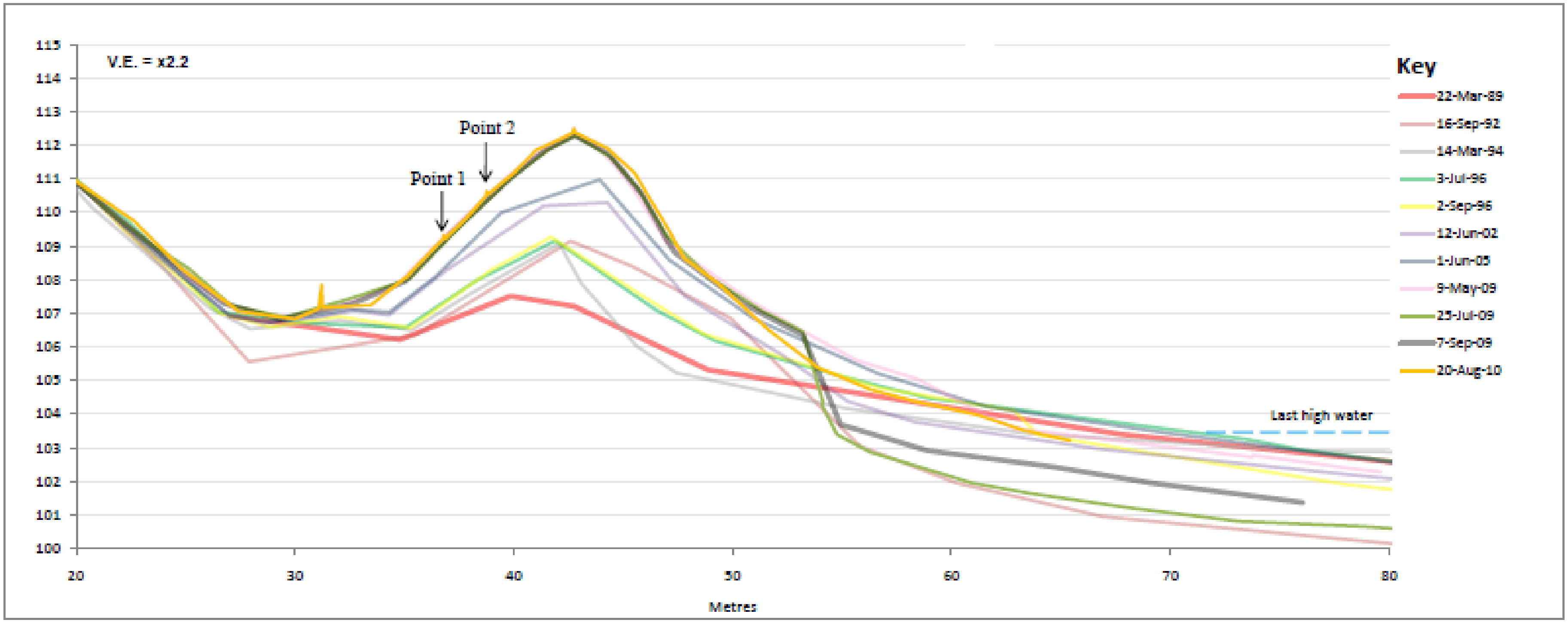

Figure 5.2: The 21-year dune profile record of St Kilda Beach, highlighting continued dune progradation and accretion since March 1989, was used to approximate the age of the marram grass seed bank. Cores were sampled from Points 1 and 2 which have been highlighted.

Allan's Beach, Otago Peninsula

Allan's Beach is located on the south coast of the Otago Peninsula, at the mouth of Hoopers Inlet, where it is generally exposed to west-northwest winds (Figure 1.5). These winds have resulted in the formation of a prograded foredune barrier adjacent to the floodtide delta, which is the main source of sediment for dune formation. The dune system consists of low dunes interspersed with hollows (Johnson, 2004) and is dominated by marram grass and tree lupin (*Lupinus arboreus*). The area of interest at Allan's Beach was a set of four parallel dune ridges situated on the north-west facing side of the beach (Figure 5.3), whose formation will be described later in this chapter (section 5.4.2). These ridges are relatively sheltered from the effects of regular wave action originating mainly from the southeast (McLean, 1967), and are almost completely colonised by marram grass and tree lupin. The possession of an aerial photographic record dating back to 1982 represents a unique opportunity to reconstruct dune development at Allan's Beach, which can be used as a proxy for ageing the marram grass seed bank over 28 years. Allan's Beach therefore provides a parallel line of inquiry to the St Kilda investigation in determining the longevity and nature of the marram grass seed bank.

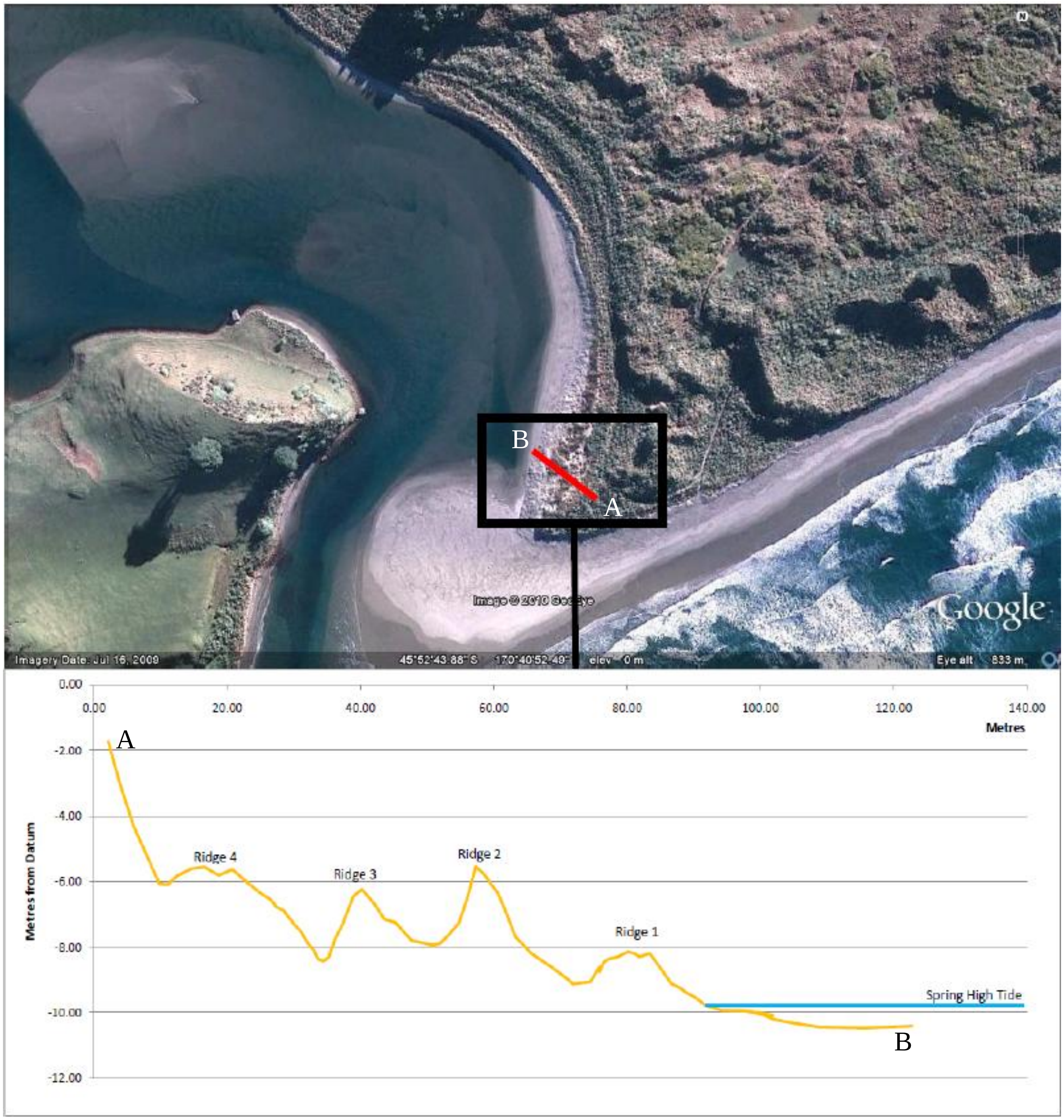

Figure 5.3: The study site at Allan's Beach (black rectangle). The profile line is marked by the red line within the study site, with points A and B clearly shown on both the profile line and accompanying profile which was collected on July 23rd, 2010.

5.3.2 St Kilda core samples

The section of dune sampled at St Kilda has a history of repeated topographical surveys from March 1989 to August 2010. Figure 5.2 shows the topographical changes in the St Kilda dune profile over time, which provides a strong link between depth and depositional age of the sediment. The assumption behind the sampling strategy therefore is that at any given depth, any recovered seed will be within a specific age range.

Three cores were taken from the field site on two separate dates, August 20th 2010 (core A1) and September 15th 2010 (cores A2 and B). Cores A1 and A2 were taken two metres north and south of the dune profile line at Point 1 and core B was taken two metres to the north of the line at Point 2. Core B was taken further upslope at Point 2 in order to reduce error in the seed bank age/depth correlation associated with movement away from the measured profile. To age the seed bank, two separate age classifications were used for Points 1 and 2. The differences in age classifications were required because the different spatial positions of Points 1 and 2 resulted in slight changes to the seed bank age/depth correlation. At Point 1 the age of the seed was split into four age groups: 1) 2010 - 2002; 2) 2002 - 1996; 3) 1996 - 1989; and 4) pre-1989. At Point 2 seed bank age was split into six age groups: 1) 2010 - 2005; 2) 2005 - 2002; 3) 2002 - 1996; 4) 1996 - 1992; 5) 1992 - 1989; and 6) pre-1989. These categories and their corresponding depths are summarised for Points 1 and 2 in Table 5.1.

Table 5.1: A summary of the age groups of recovered seed at Points 1 and 2 and their corresponding sampling depths.

Point	Age group	Depth (metres)
1	1	0 – 1
	2	1 – 2
	3	2 - 2.5
	4	2.5 – 4.5
2	1	0 – 1
	2	1 – 1.5
	3	1.5 – 2.5
	4	2.5 – 3
	5	3 – 3.5
	6	3.5 – 4.5

Each core was collected in continuous increments (henceforth called sub-samples) ranging between 6cm to 42cm, with an average of 12.4cm. When collecting each sub-sample it was particularly important to core to a precise depth because this determined the age of any recovered seed. This was achieved by using the pegs marking Points 1 and 2 as datums and extending a builder's level between the surveyed datum and the corer. It is also important to note that for core A1, sampling commenced at 49cm depth, rather than 0cm because the surface topography needed to be levelled to establish a level working surface. Care was also taken to avoid disturbance of sand at the top of the core to prevent contamination by seed from the current years' crop. The number of sub-samples, actual core depths and total depth of each core are summarised in Appendix B and will not be presented here. The number of seeds per 10 m^3 was also calculated, for each core and for St Kilda in general, in order to provide some idea of the density of seed in the St Kilda dune system. This calculation rounded the values to the nearest whole number and 10 m^3 was used as a unit to produce more logical density values i.e. 3 seeds per 10 m^3 rather than 0.05 seeds per m^3. A worked example is provided in Appendix C.

Once each sub-sample had been collected, it was bagged and labelled before storage in cool, dry conditions. Each sub-sample was then dried over a 24 - 48 hour period in a *Contherm* oven at 35°C prior to sieving. This extended period of drying under a low temperature was used to dry the sand samples completely, allowing for more efficient sieving, without killing the seeds by high temperatures. The sub-samples were then sieved using a stack of sieves consisting of a base, a 1 mm and 1.4 mm mesh. These sieve sizes captured both seeds still contained within the glumes and those that had shed this outer layer. Once seeds had been isolated, the depth and seed bank age of the sub-sample was recorded and the seeds were immediately transferred to 90mm Petri dishes for germination tests under the same regime as the test for germinability (Chapter 3). Before germination tests commenced, the outer structures of the seeds were removed because this was found to result in the greatest rate of germinability of seed in Chapter 3.

5.3.3 Allan’s Beach core samples

A total of eight cores were collected from Allan’s Beach on July 23rd 2010 and each of these were sub-sampled at three depths, 0 – 30 cm, 30 – 60 cm and 60 – 100 cm (24 sub-samples). This made both handling and separation of the surface layer from the mid and lower layers easier. Each core was taken two metres to the north of the surveyed profile line (Figure 5.3) for similar reasons to the method used at St Kilda. Once collected, the Allan’s Beach samples underwent the same post-collection process as the St Kilda samples. The density of seeds per ridge, represented as the number of seeds per 10 m^3, was also calculated for the Allan’s Beach investigation and using the same method as the St Kilda investigation.

5.3.4 Allan’s Beach dune formation

The historic development of the four parallel dune ridges at Allan’s Beach was reconstructed using a combination of ArcGIS and a set of six aerial photographs taken in 1982, 1985, 1990, 2000, 2001 and 2006, which were sourced from New Zealand Aerial Mapping. An image from Google Earth taken in 2009 was also used as the most recent record of dune ridge development. These were scanned and georeferenced in ArcGIS using six ground control points scattered as evenly as possible over the area of interest. These had a RMS error range between 0.0008 and 0.0017 and an average RMS error of 0.00024. Once the images had been georeferenced, a polyline shapefile was created which manually plotted the four dune ridges that were visible in the 2009 image. A point shapefile was also created to denote a solitary pine tree (*Pinus radiata*), which was used as the reference point to locate the datum of the Allan’s Beach survey line. Once the four dune ridges had been plotted, these were overlaid onto the aerial photographs of Allan’s Beach from the preceding years and the historical development of the dune ridges was reconstructed.

5.4 Results

5.4.1 St Kilda cores

Seeds were recovered from the St Kilda cores across a range of depths and ages, providing this study with seed bank data up to and potentially beyond 21 years. The total number and corresponding age of those seeds recovered from the three cores is presented in Table 5.2. Within core A1, seeds were generally found across a range of depths, although the number of seeds recovered decreased relatively quickly with increasing depth (n = 38). This was highlighted by the recovery of 31 seeds within the first metre compared to seven in the final three metres. Seeds recovered within the top one metre of core A1 were less likely to germinate (84% germination) compared to a those below one metre depth (100%). Core A2 had a much lower rate of recovery compared to the other two cores (n = 7). This may have been due to an absence of flowering individuals at the time the strata was deposited because of the spatial heterogeneity of flowering in marram grass across the foredune. Seeds were recovered over a range of depths including 0 – 1 m, 1 – 2 m, 2 – 3 m and 3 – 4 m. In contrast to cores A1 and B seeds recovered from 2 – 3 m did not germinate upon further testing. However, these seeds were black when recovered and were unlikely to have been viable. Seeds recovered from core B came from two main depth ranges, 0 – 2 m and 3 – 4 m, with no other depths yielding seeds during coring (n = 31). Similarly to core A1, seeds in the upper layers of the core tended to show a lower rate of germination compared to the lower layers.

The depths and numbers of recovered seed from each core in Table 5.2 are diagrammatically presented in Figures 5.4, 5.5 and 5.6. For ease of interpretation, in each of these figures, only four profile lines have been included, March 1989, March 1994, June 2002 and August 2010. The last high water and seaward front of vegetation have also been included to give a spatial perspective of core location, relative to the ocean. On the August 2010 profile line, small ‘blips’ can also be seen. The first, much larger spike is an old datum used in a monitoring program of the St Kilda dune in the late 1980s (M. Hilton, Pers. Comm.), followed by the pegs at Points 1 and 2 and finally the dune crest. Each core is clearly marked and the depths at which seeds were recovered are represented by dotted lines extending out from the core. Finally all recovered seeds are indicated on the diagram, with those that germinated being represented by a green circle and those that were recovered but did not germinate being represented by a black circle.

Table 5.2: A summary of the depths from which seeds were recovered in cores A1, A2 and B from St Kilda Beach. The number of seeds that were recovered and subsequently germinated are also included as well as the corresponding estimation of seed bank age.

Core	**Sub-sample depth (cm)**	**Number of seeds recovered**	**Number of seeds germinated**	**Estimated age of recovered seed (years old)**
A1 (n=38)	77 – 88.5	22	19	0 – 8
	88.5 – 99	9	7	0 – 8
	99 – 117	2	2	8 – 14
	117 - 131	1	1	8 – 14
	131 – 143	1	1	8 – 14
	291.5 – 303	1	1	21+
	352.5 – 364.5	2	2	21+
A2 (n=7)	0 – 40	3	2	0 – 8
	100 – 116	1	1	8 – 14
	267 – 276	2	0	21+
	369 – 379	1	1	21+
B (n=31)	0 – 42	6	6	0 – 5
	42 – 66	6	5	0 – 5
	81 – 101	5	3	0 – 5
	101 – 123	3	3	5 – 8
	123 – 143	2	2	5 – 8
	143 – 161	2	1	5 – 8
	161 – 185	1	1	8 – 14
	300 – 309	1	1	18 – 21
	309 – 318	1	1	18 – 21
	322 – 335	1	1	18 – 21
	335 – 345	1	1	18 – 21
	390 – 401	2	1	21+

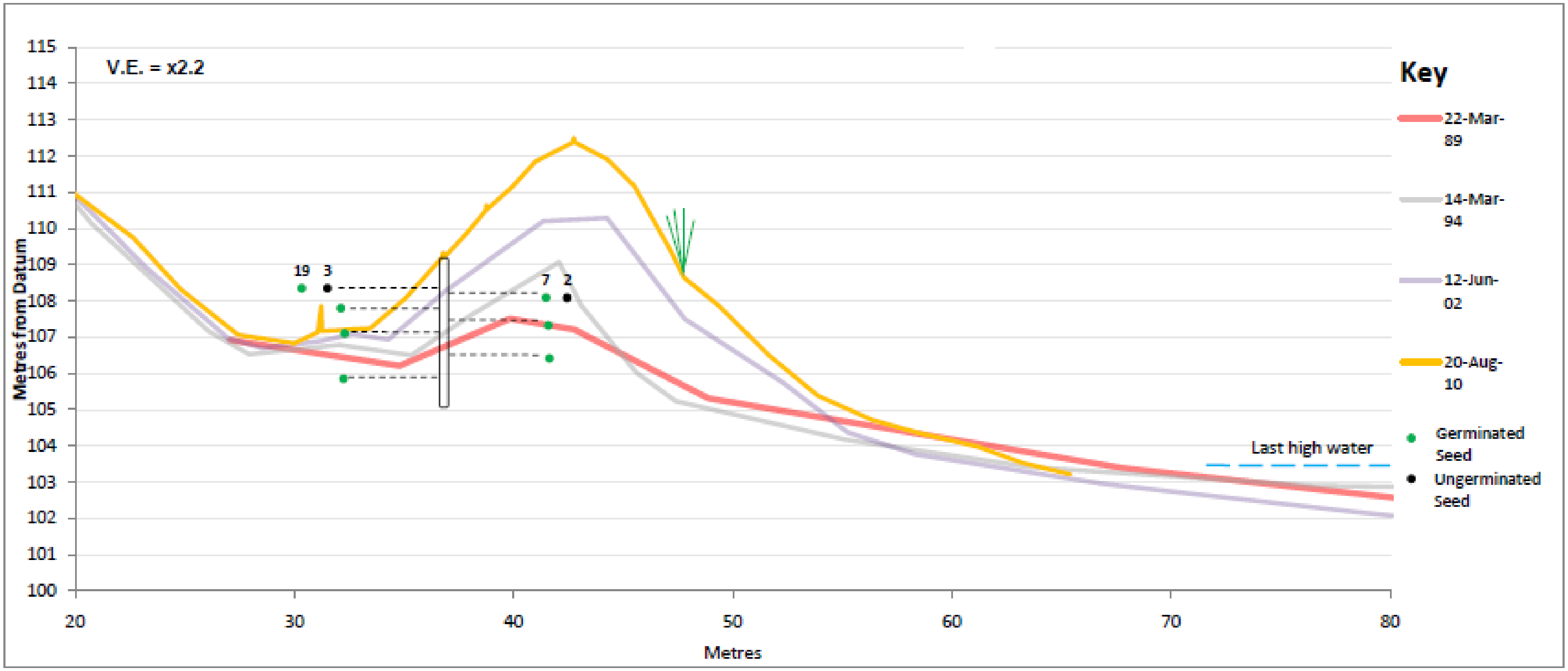

Figure 5.4: The number of seeds recovered and the depths at which they were recovered in core A1. The green circles represent those seeds that germinated and the black circles represent those seeds that were recovered but did not germinate. For depths where more than five seeds were recovered, numbers were used to indicate the number of seeds that were recovered and germinated versus those that were recovered but did not germinate.

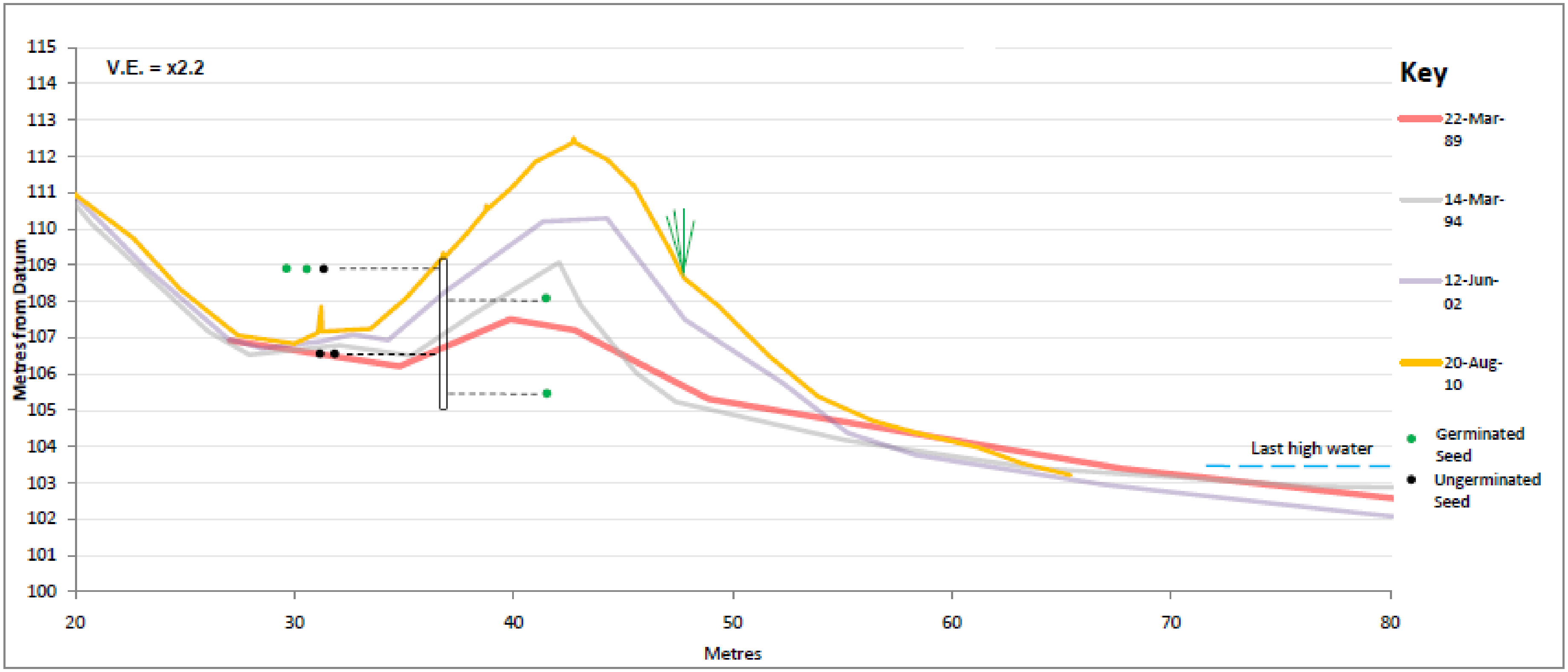

Figure 5.5: The number of seeds recovered and the depths at which they were recovered in core A2. See Figure 5.4 for further explanation of symbols.

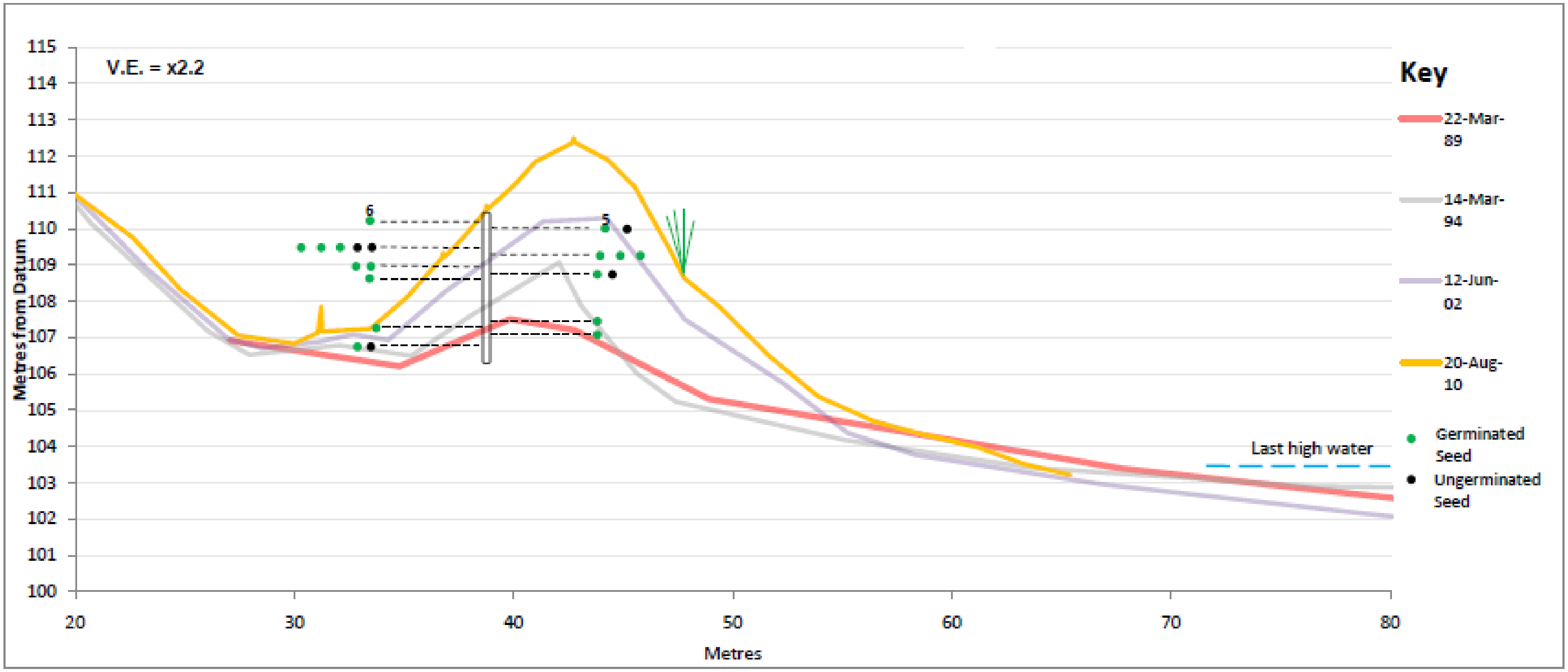

Figure 5.6: The number of seeds recovered and the depths at which they were recovered in core B. Note that the core location is further up the dune profile, graphically highlighting the difference in spatial location of Points 1 and 2. See Figure 5.4 for further explanation of symbols.

Seeds recovered in the three cores taken from St Kilda were split into four age groups for cores A1 and A2 and six age groups for core B. In cores A1 and A2, the greatest number of recovered seeds fell within age group one (0 - 8 years old), whilst similar numbers of seeds were recovered from age groups two (8 - 14 years old) and four (21+ years old). None of the seeds recovered from cores A1 and A2 fell within age group three (14 - 21 years old). With respect to germination, age group one (n = 34) showed the lowest percent germination 82%. Age group two (n = 5) had 100% germination and age group four (n = 6) showed 67% germination (Figure 5.7).

The greatest number of seeds recovered from core B fell within age group one (0 - 8 years old; n = 17). Seven of the recovered seeds fell within age group two (5 - 8 years old), four fell within age group five (18 - 21 years old) and age groups three (8 - 14 years old) and six (21+ years old) contained one seed each. No seeds were recovered from age group four (14 - 18 years old). Percent germination was relatively low in age group one, (82%; n = 17), while age group two also failed to reach 100% germination with six out of seven seeds germinating (86%). Seeds recovered from age groups three (n = 1), five (n = 4) and six (n = 1) however all showed 100% germination (Figure 5.8).

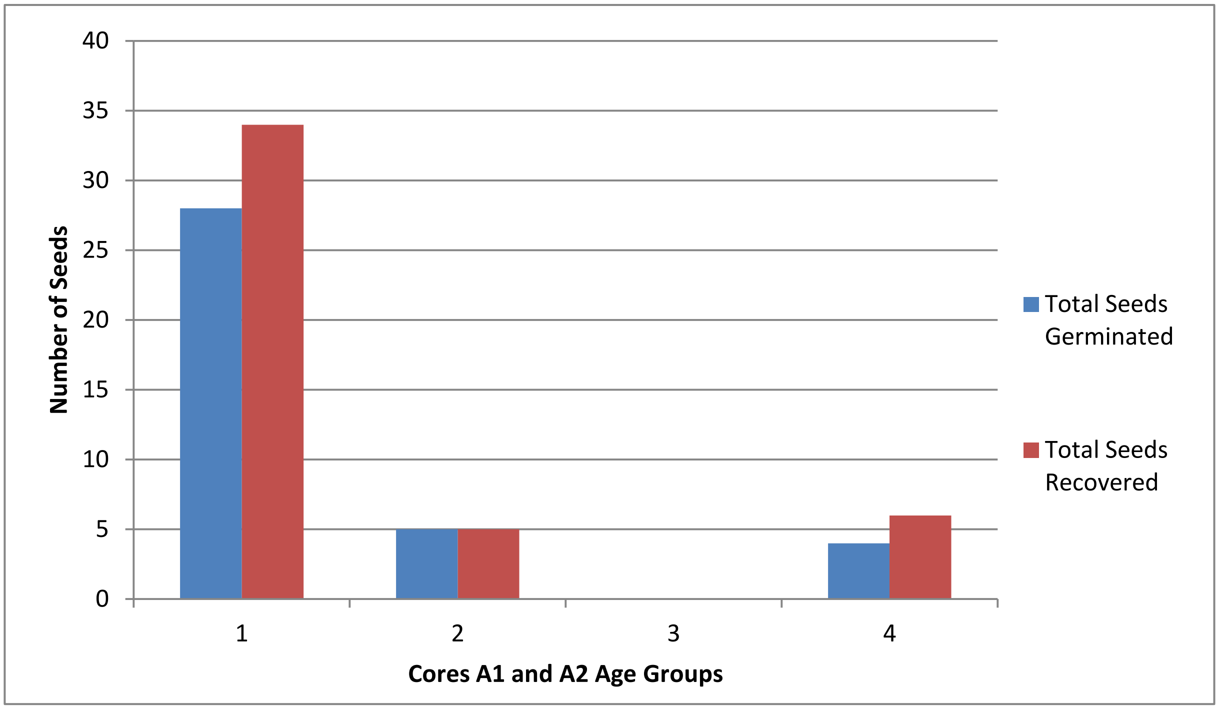

Figure 5.7: The age groups from which seeds were recovered and subsequently germinated in cores A1 and A2 taken from St Kilda Beach. The estimated ages of each group are as follows: 1) 0 - 8 years old; 2) 8 - 14 years old; 3) 14 - 21 years old; and 4) 21+ years old.

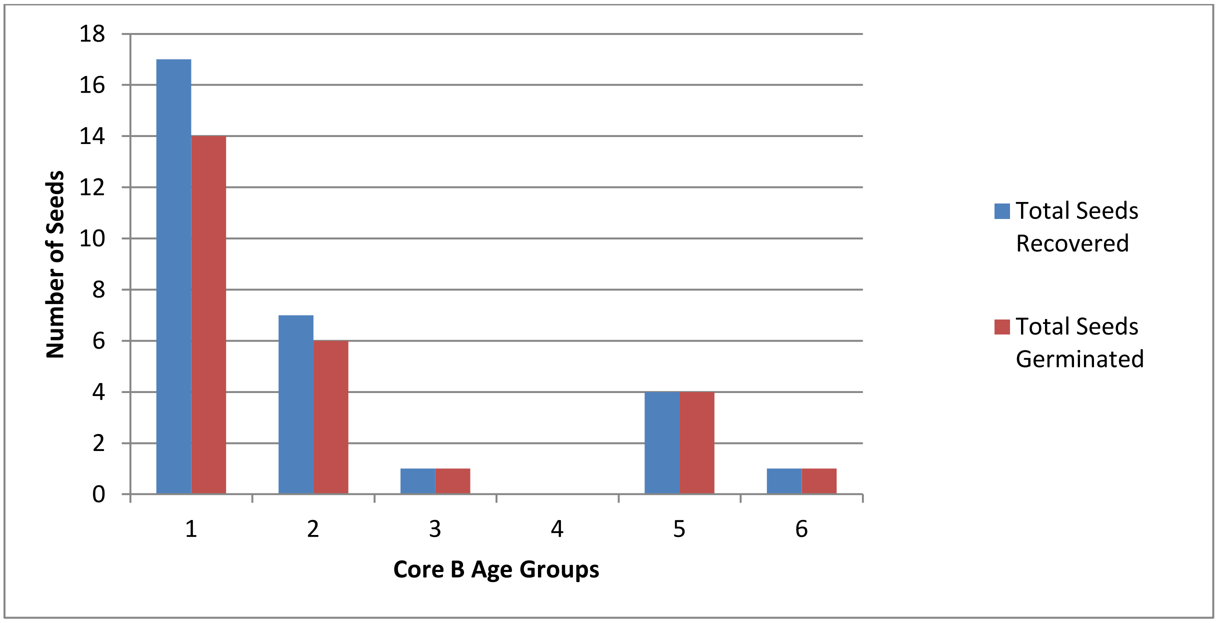

Figure 5.8: The age groups from which seeds were recovered and subsequently germinated in core B taken from St Kilda Beach. The estimated ages of each group are as follows: 1) 0 - 5 years old; 2) 5 - 8 years old; 3) 8 - 14 years old; 4) 14 - 18 years old; 5) 18 - 21 years old; 6) 21+ years old.

Table 5.3 presents a synthesis of the age and the germinability of seeds that were recovered from cores A1, A2 and B. The greatest number of germinable seeds that were recovered were 0 - 8 years old (n= 48). For the other age groups 8 – 14 years old, 18 – 21 years old and 21+ years old there were a similar number of germinable seeds recovered (six, four and five seeds recovered respectively). No seeds between the ages of 14 – 18 years old were recovered from the three cores at St Kilda. Although the majority of germinable seeds recovered were relatively young, the presence of 15 seeds greater than eight years old and five seeds greater than 21 years old is a very significant result. These results also indicate relatively high germinability among buried seeds, with age groups 8 – 14 and 18 – 21 showing 100% germination. Seeds aged between 0 and 8 years showed 82.8% viability whilst seeds aged 21+ years showed the lowest viability of 71.4%.

Table 5.3: A synthesis of the ages of all germinable seeds that were recovered from cores A1, A2 and B at St Kilda Beach. Note that none of the recovered seeds were aged between 14-18 years old.

Age of seeds (years)	**Number of seeds recovered**	**Number of seeds germinated**	**Percent germinability**
0 – 8	58	48	82.8%
8 – 14	6	6	100%
18 – 21	4	4	100%
21+	7	5	71.4%

5.4.2 Reconstructing Allan's Beach dune formation

The photographic record of Allan's Beach, obtained for this study, consisted of a 2009 image retrieved from Google Earth (Figure 5.9) and six aerial photographs taken in 2006 (Figure 5.10), 2001 (Figure 5.11), 2000 (Figure 5.12), 1990 (Figure 5.13), 1985 (Figure 5.14) and 1982 (Figure 5.15). The best approach to reconstructing historic dune ridge formation was retrospective, starting from 2009 and working backwards through time. This makes it easier to isolate the approximate date at which each dune ridge was present in the photographic record and therefore indicate the beginning of seed bank formation. In Figure 5.9 (2009), the four dune ridges are marked on the 2009 image, with ridge 1 being closest to the water's edge and ridge 4 furthest from the water's edge (Figure 5.3). This is the most recent of image in the photographic record and will be used as a reference for the identification of the dune ridges in earlier aerial photographs.

Ridge 1 was not present in 2001, and therefore any seed recovered from this ridge will be no older than three years and possibly as young as one year old. This age range is supported by previous observations that suggest that ridge 1 formed in 2007 as an incipient foredune, with the flowering of marram grass not occurring until 2009 (M. Hilton, Pers. Comm.). The 2006 image points to the recent formation of ridge 2 which is highlighted by its seaward nature compared to ridge 3. An expanse of bare sand between ridges 2 and 3, in Figure 5.10 (2006), suggests that ridge 2 may have been an incipient foredune in 2006. This is supported by both the 2001 and 2000 images (Figures 5.11 and 5.12), where ridge 2 is no longer evident on the photographic record. Ridge 3 and ridge 4, however still appear to be present at this stage of dune development.

In 1990 (Figure 5.13), ridge 3 was probably not present. This conclusion is based on two observations; firstly that the tidal currents in the estuary had eroded the dune system very close to the estimated location of ridge 3, which may have resulted in its erosion. Secondly, there is no dark pixilation in Figure 5.13, which normally indicates vegetation. Although incipient foredunes do not always require vegetation to begin their formation, the distinct lack of vegetation precludes the idea that marram grass could have formed a seed bank on this dune ridge in 1990. Therefore ridge 3 likely formed in the intervening years between 1990 and 2000 and any seed recovered could be from 0 – 20 to 0 – 10 years old depending on when dune formation and marram flowering began. With respect to the formation of ridge 4, the photographic records suggest it was present in the earliest image (Figure 5.15). From 1985 (Figure 5.14) however, there appears to be a thick cover of vegetation at the estimated location of ridge 4. Although the vegetation is not identifiable, its dark pixilation, indicating dense vegetation cover, would suggest the presence of another plant species other than marram grass. Marram grass was therefore unlikely to have been present as a reproductive population at this stage of development.

Figure 5.9: The four dune ridges at Allan’s Beach in 2009. The area of interest is marked by the red box and the four ridges are represented by the orange lines. These were numbered 1 to 4 with 1 being closest to the shoreline and 4 being furthest from the beach. The pine tree used as a reference point for locating the survey datum is also marked as a green circle.

Figure 5.10: An aerial photograph of Allan's Beach, taken in 2006, which shows the historical development of the four sampled dune ridges.

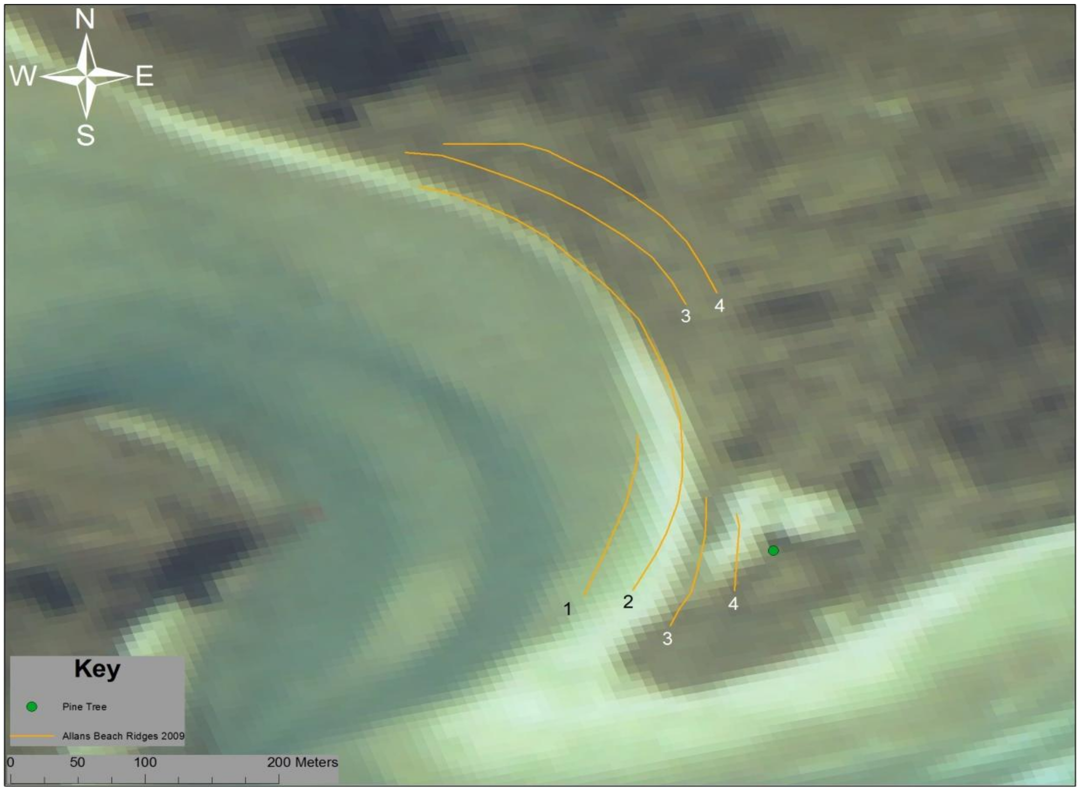

Figure 5.11: An aerial photograph of Allan's Beach, taken in 2001, which shows the historical development of the four sampled dune ridges.

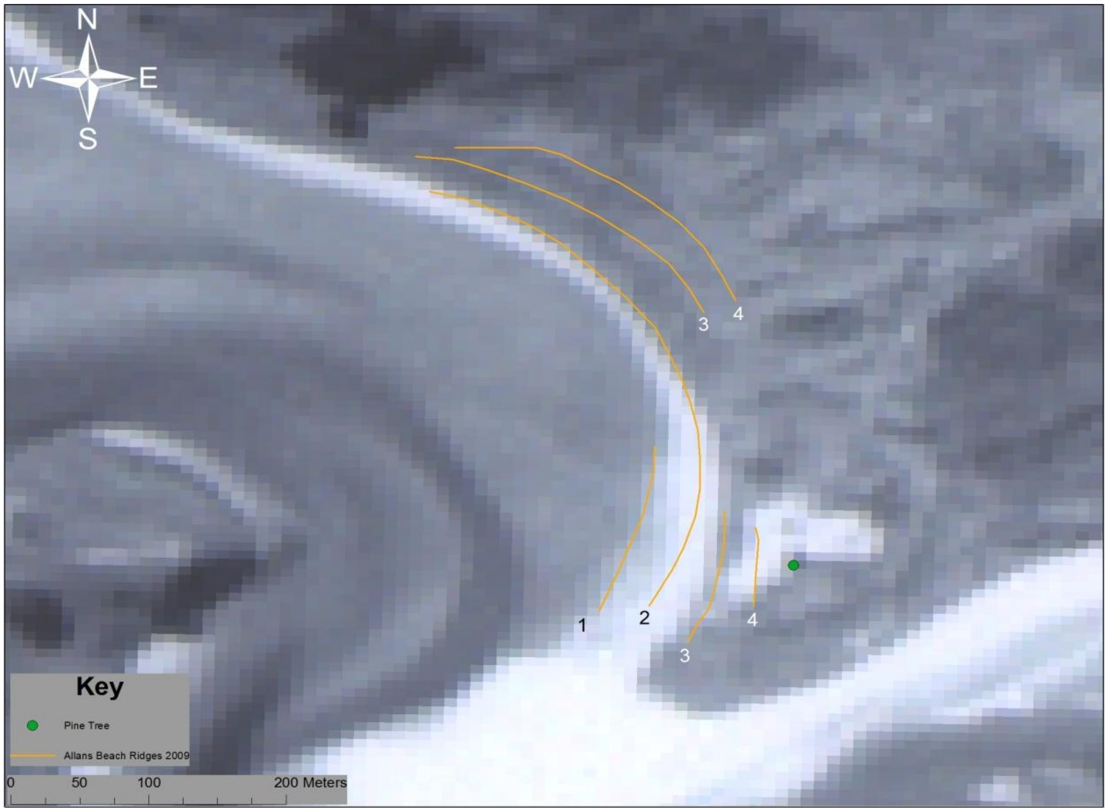

Figure 5.12: An aerial photograph of Allan’s Beach, taken in 2000, which shows the historical development of the four sampled dune ridges.

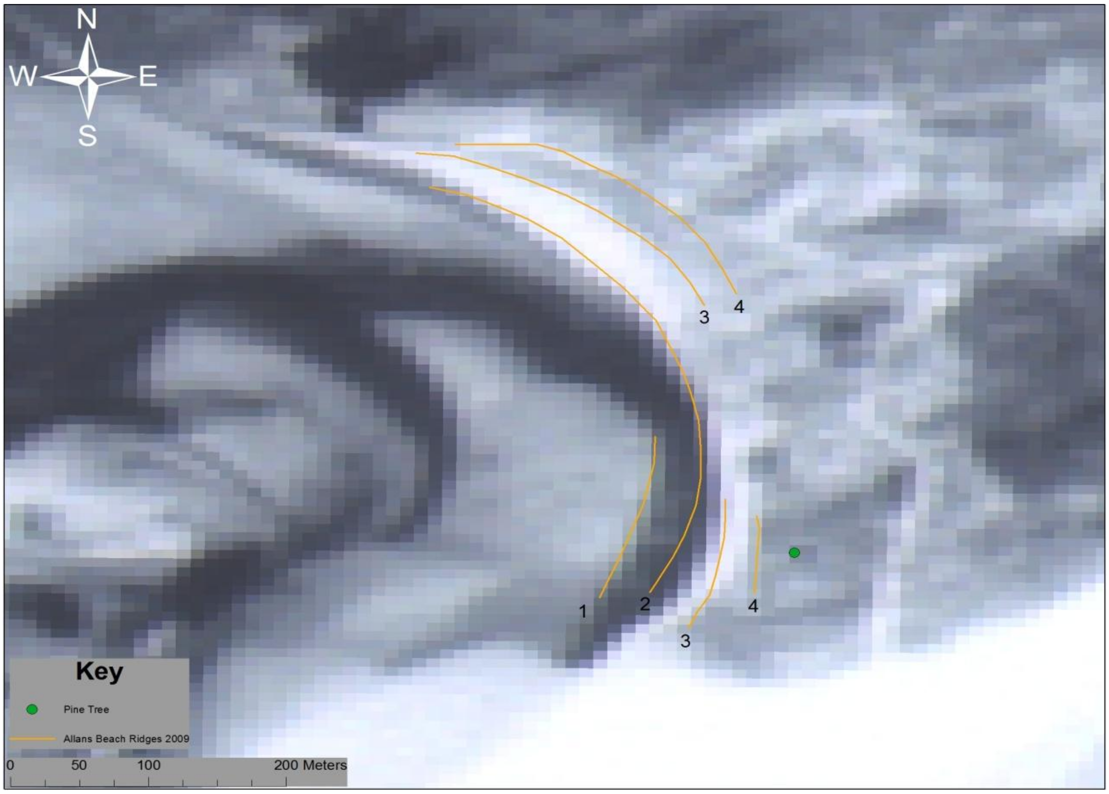

Figure 5.12: An aerial photograph of Allan’s Beach, taken in 1990, which shows the historical development of the four sampled dune ridges.

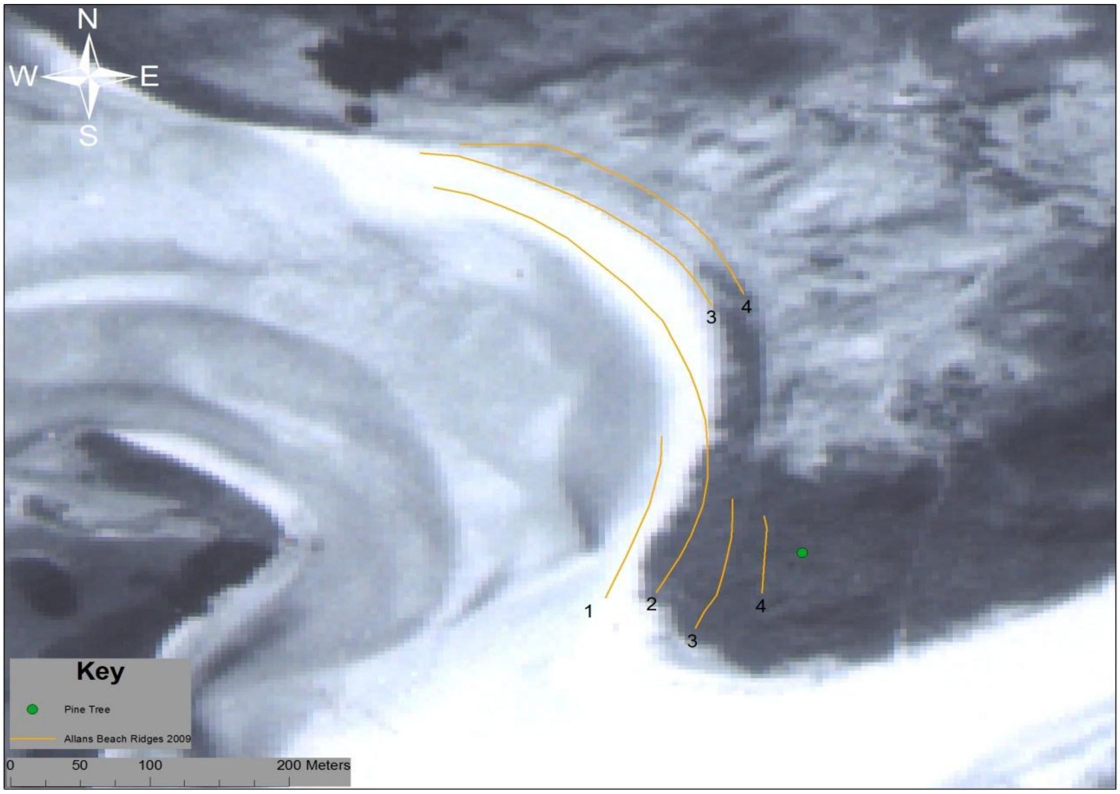

Figure 5.13: An aerial photograph of Allan's Beach, taken in 1985, which shows the historical development of the four sampled dune ridges.

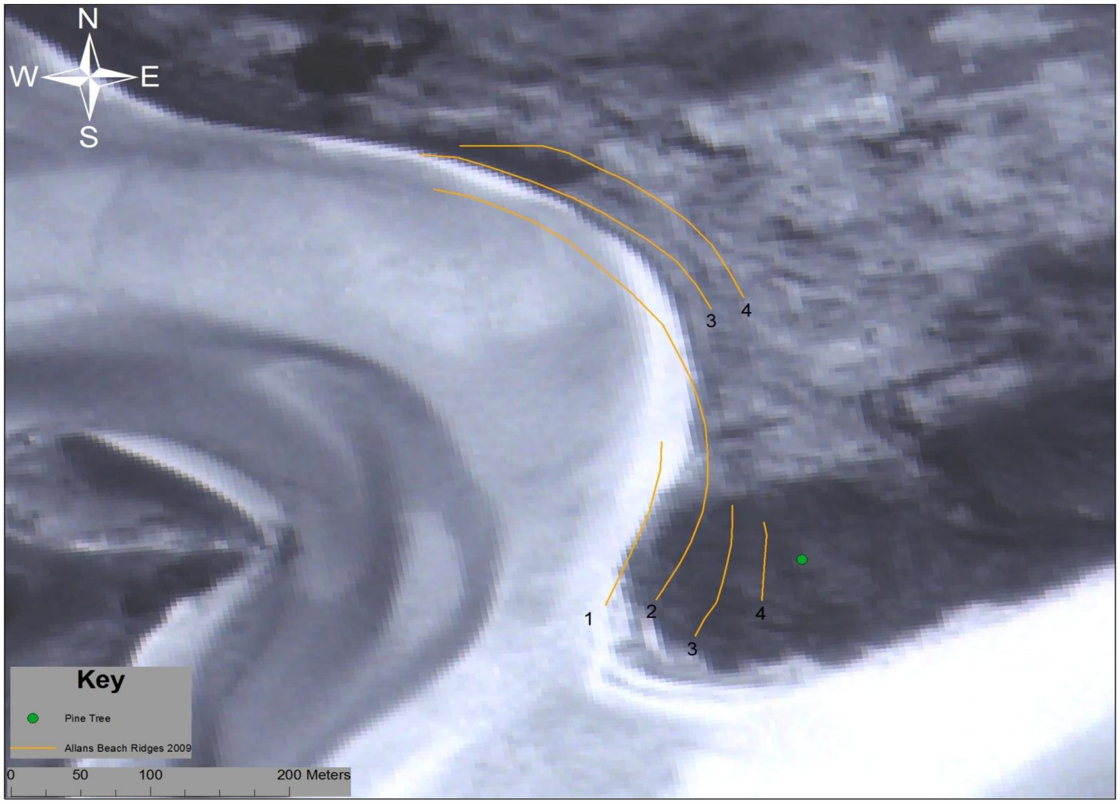

Figure 5.14: An aerial photograph of Allan's Beach, taken in 1982, which shows the historical development of the four sampled dune ridges.

Seeds were recovered from ridges 1, 2 and 3 at Allan's Beach however no seed was recovered at ridge 4 (Table 5.4). The greatest numbers of seeds recovered were 19 and 20 seeds from ridges 2 and 3 respectively, whilst three were recovered from ridge 1. There was little difference with respect to percent germination between ridges 2 and 3 (94.7% and 85% respectively) while ridge 1 showed a lower percent germination (66.7%), although the number of recovered seeds in ridge 1 was fewer than ridges 2 and 3. The estimated ages of the dunes suggests that the majority of seeds recovered and subsequently germinated from Allan's Beach were between 0 and 20 years old, with no evidence of a seed bank more than 20 years old.

Table 5.4: A comparison of the number of seeds recovered from each dune ridge at Allan's Beach and the subsequent number that germinated.

Ridge number	Number of seeds recovered	Number of seeds germinated	Percent germinability	Estimated age of seed (years old)
1	3	2	66.7%	0 - 1
2	19	18	94.7%	1 - 4
3	20	17	85%	4 – 20
4	0	0	N/A	20 – 28

Unlike the investigation at St Kilda, seed bank age at Allan's Beach was unable to be correlated with depth. Instead the seed bank was aged according to the development of foredune ridges and the subsequent cores were divided into three arbitrary sub-samples. The estimated age of seeds recovered in the upper sub-sample of the core (0 – 30 cm) is therefore much less certain compared to the other sub-samples, because of the risk of recent seed fall and burial near the surface. Conversely, those seeds recovered from the two deeper sub-samples (30 – 60 cm and 60 – 100 cm) are more likely to be the estimated age because this risk is reduced with increasing depth of burial.

Figure 5.16 indicates the depths at which seeds were recovered within each of the four dune ridges. In ridge 1, there was a lack of seed recovery in the 0 – 30 cm sub-sample, with seed recovery beginning in the 30 – 60 cm sub-sample. The rate of recovery therefore increased slightly with increasing depth. In ridge 2, the greatest recovery of seeds occurred in the upper layers of the core, with a gradual yet consistent decline in rate of seed recovery with increasing depth. Ridge 3 followed a similar pattern to ridge 2 with the greatest recovery of seeds occurring in the upper sub-section of the core. In contrast to ridge 2 however, the rate of seed recovery in ridge 3 declined dramatically with increasing depth. There was no seed recovery in ridge 4.

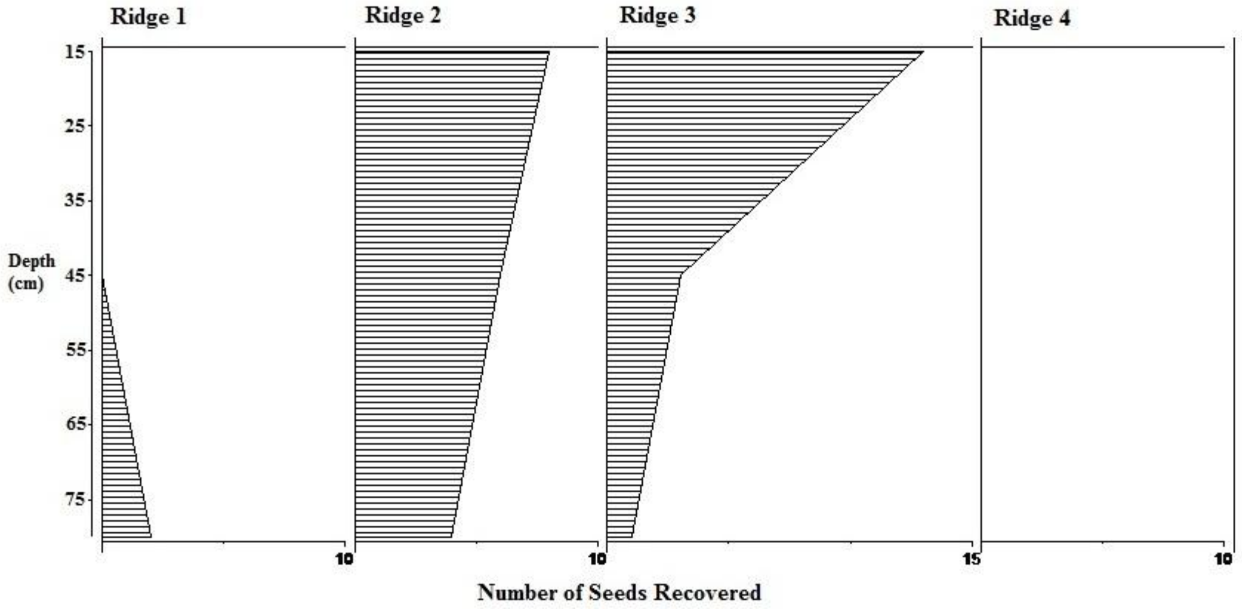

Figure 5.15: A summary of the depths at which seed was recovered from each of the dune ridges at Allan's Beach and the numbers of seeds recovered.

5.4.3 The density of seed at St Kilda and Allan's Beach

The density of seeds per 10 m^3 in each of the St Kilda and Allan's Beach cores as well as the overall density of seeds is presented in Table 5.5. The seed density values were rounded to the nearest whole number to provide a more logical density value. At St Kilda, core A1 seed density was ~3 seeds per 10 m^3. Core B showed a similar seed density (~2 seeds per 10 m^3) whilst core A2 had a lower density (~1 seeds per 10 m^3). Overall the density of seed at St Kilda was ~2 seeds per 10 m^3. At Allan's Beach, the density of seed was ~1, ~3 and ~3 seeds per 10 m^3 for dune ridges 1, 2 and 3 respectively. No seeds were recovered from dune ridge 4 and therefore a density value was not calculated. Therefore the overall density of seed at Allan's Beach (of dune ridges that yielded seed) was ~2 seeds per 10 m^3.

Table 5.5: A summary of the densities of seed in each of the cores and dune ridges as well as the overall density of seed at St Kilda Beach and Allan’s Beach. The seed density values were also rounded to the nearest whole number.

Study site	**Core/Ridge #**	**Seed density (10 m^{-3})**	**Overall seed density (10 m^{-3})**
St Kilda	A1	3	
	A2	1	
	B	2	2
Allan’s Beach	1	1	
	2	3	
	3	3	2

5.5 Discussion

5.5.1 Evidence for a seed bank in marram grass

This study was presented with unique opportunities to investigate the nature and longevity of the marram grass seed bank in two dune systems of southern New Zealand. The findings of this chapter have clearly shown that marram grass is capable of forming a seed bank that may persist up to and potentially beyond 21 years. This is in contrast with the findings of previous research and represents a very significant finding with respect to marram grass seed ecology.

There is a perception, especially in key studies relating to marram grass ecology, that sexual reproduction is less important than vegetative (Huiskes, 1979; Maun, 2009). The findings of the current study and other research however have contradicted this school of thought. Only two studies have investigated the longevity of *Ammophila* seed banks. Zhang and Maun (1994) estimated that *Ammophila breviligulata* seed persisted for approximately 3.24 years according to rates of decay in artificially buried seeds. Konlechner and Hilton (2009) found that, in southern New Zealand, the *Ammophila arenaria* seed bank provided a source of re-invasion for ‘at least 9 years’ following eradication of the flowering population at Doughboy Bay, Stewart Island. The results of the current investigation into marram grass seed bank longevity far exceeded these previous two estimates. At St Kilda, recovered viable seed was aged between 0 and 21+ years old, whilst at Allans Beach, recovered viable seed was aged between 0 and 20 years old. This would suggest that marram grass eradication operations in southern New Zealand may need to be conducted in excess of 21 years following control of the flowering population. This has serious implications for marram grass eradication programs which will be discussed further in Chapter 7.

The formation of a seed bank in marram grass is a similar life strategy to many other species living in disturbed environments, where there is a high risk of mortality (Baskin and Baskin, 1998; Thompson *et al.* 1998; Zhang and Maun, 1994). The marram grass seed bank likely originates from the large numbers of seeds produced by marram grass in favourable environments, such as the foredune face (Chapter 2). These seeds generally do not disperse far from the source population despite their location in exposed, windy environments. Instead, the majority of seeds are likely to fall beneath the adult population on the foredune, especially where the established marram grass population greatly increases the roughness element of the near-surface, reducing the winds ability to disperse seed (Bagnold, 1971). This increase in surface-roughness by vegetation, coupled with the rapid rate of sand accumulation common to marram grass (Ranwell, 1972), will likely result in the timely burial of seed in conditions conducive to long-term storage. This allows for the development of a significant seed bank, particularly under the massive foredunes formed by marram grass. Investigations into seed bank density at both St Kilda and Allan's Beach have found that the density of seeds was approximately 2 seeds per 10 m^3 for both study sites. This information provides an approximate idea of the size of the marram grass seed bank in the foredunes of southern New Zealand and can be utilised by land managers when planning eradication operations.

The extended longevity of the marram grass seed bank combined with the gradual release of sand from the foredune following marram grass eradication results in a gradual process of re-invasion by seed. Hilton *et al.* (2009) investigating the rate of marram grass decay following herbicide application at Doughboy Bay, found that dying marram grass still provided significant cover for at least 2 years following spraying. This cover resulted in the gradual release of sand from the controlled region, with an increase in rate of sand loss and concommitment drift and downwind deposition not occurring until 2004 (five years after spraying began). By slowing the rate of erosion of sand from the foredune, the risk of fatal desiccation of marram grass seed from exposure to wind and solar radiation is greatly reduced. Retarding the removal of sand, also gradually exposes marram grass seed to fluctuating light and temperatures which triggers germination. This suggests that, following control, seed may still experience favourable conditions for germination and long-term storage, further highlighting the importance of monitoring in control operations.

5.5.2 Percentage of viable seeds

Although some of the recovered seeds in this investigation were aged in excess of 21 years, these seeds only present a threat to control operations if they are viable. Seed recovered from St Kilda ranged in germinability from 71.4% to 100% whilst seed recovered from Allan's Beach showed germinability ranging between 66.7% and 94.7%. The variation in seed age and germinability between the two dune systems suggests that there may be local variation in the marram grass seed bank in southern New Zealand. However, the Allan's Beach data generally supports the findings of the St Kilda study and highlights the risk that marram grass seed poses with respect to re-invasion over a relatively long period of time.

The viability of recovered seed in the current study also appeared to exceed estimations of viability in previous studies of *Ammophila* seed. Krajnyk and Maun (1982) found that *Ammophila breviligulata* often produced low quality seeds (between 28% - 48% viability), which they suggested was a result of self-incompatibility, pollen shortages, biotic agents and adverse environmental conditions during seed formation. Van der Putten's (1990) investigation showed that marram grass seed germinability ranged between 14% - 94% depending on pre-treatments and germination conditions. Pope (2005) found that germinability in marram grass seed, collected from a local population in southern New Zealand, ranged between 2.91% and 40.08% depending on the state of the seed, i.e. fresh or dry, and the year in which it was collected. This suggests that the seed recovered during the current investigation was stored under natural conditions at generally the upper limits of marram grass seed viability found by other studies.

In the St Kilda seed bank investigation, seed aged between 0 and 8 years old showed a reduced germinability compared to seed aged between 8 to 21 years old. This suggests that not all of the seed recovered from the upper layers at St Kilda was of an optimum quality. As seeds age and are buried under a deeper layer of sand, the seeds of inferior quality are more likely to decay, leaving a population of seeds that may be larger and longer lasting (Zhang and Maun, 1994). However, as marram grass seeds aged past 21 years, it was apparent that even these higher quality seeds begin to decay despite favourable storage conditions. This loss is a natural part of the decomposition process and would be expected within any seed bank population (Zhang and Maun, 1994). In the current study, seed aged 21+ years had a germinability of 71.4% compared to 100% germinability in seed aged between 18 to 21 years old. This relatively rapid decline in germinability may suggest that marram grass seed does not survive for an extended period after 21 years. Seed obtained from a herbarium specimen collected from St Clair in 1965 (45 years old) may shed some light on the long-term viability of marram grass seed. Of a total sample of 20 seeds, two showed initial signs of germination under the same conditions used to germinate seeds in the current study (Chapter 3). In all cases however the radicle ceased growing and the plumule failed to emerge indicating a limited long-term viability in marram grass seed (J. Lord Pers. Comm.).

5.5.3 Uncertainty of data

The seed bank data collected from both St Kilda and Allan's Beach, although potentially significant, should also be considered in light of the uncertainty related to the techniques used to collect the seed. As described previously in this chapter, seed from St Kilda was collected from cores where depth corresponded to specific ages. Ageing of buried seeds in this case relied on measurements of changes in the surface level of the foredune over the 21 year period. Uncertainty in this case occurs during the collection of the cores, where sampling of sand to specific depths may not have been completely accurate. This may have been due to error in reading measurements by the research team or a result of disturbed sand falling back into the core. It is thought however, that the ageing of seeds at St Kilda was a generally accurate procedure, providing an ideal opportunity for sampling a marram grass seed bank of known age.

The ageing of the seed bank at Allan's Beach (i.e. 4 to 20 years old) was much less evenly distributed compared to St Kilda. This degree of uncertainty relating to seed bank age arose largely from the low temporal and spatial resolution of the available aerial photographic record, making the reconstruction of dune ridge development difficult. This is perhaps best exemplified by the 10-year gap between 1990 and 2000 aerial photographs. This occurred at a point in dune development which was crucial to the ageing process and consequently reduced the accuracy of seed bank ageing at Allan's Beach. Despite this relative inaccuracy, the data obtained from Allan's Beach provides a valuable second independent estimation of the potential age of the marram grass seed bank and the change in germinability with increasing age.

5.6 Chapter summary

Planisek and Pippen (1984) concluded that coastal dune species do not form seed banks in the coastal environment. This was disputed by Zhang and Maun (1994) who found evidence of persistent seed bank formation in seven plant species along the shores of the Great Lakes, Ontario, Canada. It was proposed that methodological errors in Planisek and Pippen's (1984) study were most likely the cause of their conclusions rather than the lack of seed bank formation in coastal dune systems. This is supported by Thompson *et al.*'s (1998) findings that seed persistence is selected for in disturbed environments. A study conducted by Konlechner and Hilton (2009) at Doughboy Bay, found that marram grass seedlings germinated 'at least 9 years' after the eradication of the last flowering individuals from the foredune. This evidence strongly suggests that marram grass forms viable seed banks in coastal dune environments of southern New Zealand and provides justification for the investigation of seed bank longevity in the current study.

The investigation of seed bank longevity at both St Kilda and Allan's Beach utilised dune profiles and aerial photography that had been collected over 21 and 28 years respectively. At St Kilda, a surveyed dune profile dataset spanning 21 years was used to temporally separate the layers of the foredune and thereby age seed. At Allan's Beach, the aerial photographic record was used to reconstruct dune ridge development over a 28 year period which enabled the ageing of the seed bank. These data sources provided an important and unique opportunity to carry out an investigation into seed bank longevity using methods that had not been conducted in any seed bank studies to date.

Seed collected from St Kilda was aged between 0 – 21+ years (n = 76). With respect to germinability, seeds aged 0 – 8 and 21+ showed less than 100% germinability (82.76%, n = 58, and 71.43%, n = 7, respectively), however seeds aged 8 – 21 had 100% germinability (n = 10). At Allan’s Beach, seeds were aged between 0 – 20 years old and germinability ranged between 66.67 – 94.74% (n = 42), which was lower than the seeds collected from St Kilda. This suggested local variation in the viability of seed banks in southern New Zealand.

The findings of the current study suggest that marram grass seed can survive at relatively high rates of viability for at least 21 years. This represents a very significant finding, with the previous longest estimate being ‘at least 9 years’ (Konlechner and Hilton, 2009). This has serious implications for marram grass eradication programs because, in light of the study’s findings, monitoring and eradication operations along the foredune need to continue for at least 21 years after removal of the last flowering individuals. Recommendations for ongoing marram grass eradication programs (Hilton and Konlechner, 2010), based on the findings of this chapter, will be presented in Chapter 7.

Chapter 6

The invasion process

6.1 Overview

The main aim of the current study was to determine the potential for marram grass re-invasion from the secondary dispersal and *in situ* germination of seed. The findings of the previous chapters have shown clear evidence that seed plays a key role in marram grass invasion. The development of a conceptual model of the process of marram grass invasion via seed was a key outcome of the current research. The model is based on both the findings of the current investigation into different aspects of seed ecology as well as previous studies. Currently there are no conceptual models of marram grass invasion via seed in the literature. It is therefore hoped that the development of the model will aid the study in achieving objective one by describing the process of downwind invasion via seed in a transgressive dune system in southern New Zealand. This chapter will be divided into three sections which will provide a description of the basic model components (section 6.2), an explanation of the stages of invasion (section 6.3) and a discussion of the model assumptions and future research directions (section 6.4).

6.2 The basic model

The key aspect of the model is the division of the central dune system of Mason Bay into temporal stages of marram grass invasion by seed. In Figure 6.1, the model is divided into four stages: 1) the foredune, which is considered to be the main source of seed for invasion; 2) stage 1, the maximum distance over which seed is thought to initially disperse before settling and establishing; 3) stage 2, the next part of the dune system over which seed is estimated to potentially disperse and establish in; and 4) stage 3, the final part of the dune system, over which dispersal and establishment can occur.

Dispersal and invasion are not considered in the foredune because this is an already heavily modified and invaded dune feature and thus any seed settling and establishing here is relatively inconsequential with respect to invasion into the greater dune system. The three stages were determined using data from both the current investigation and previous studies relating to: 1) how far seed is likely to travel; 2) natural barriers such as depositional lobes of the parabolic dunes and elevational steps; and 3) inferences taken from the analysis of seedling distribution patterns (Chapter 4). An explanation of the stage boundaries within the conceptual invasion model will be presented in section 6.3. Although this model cannot wholly explain the invasion process, it is hoped that it will provide the reader with an idea of the potential pathways through which invasion can occur at Mason Bay.

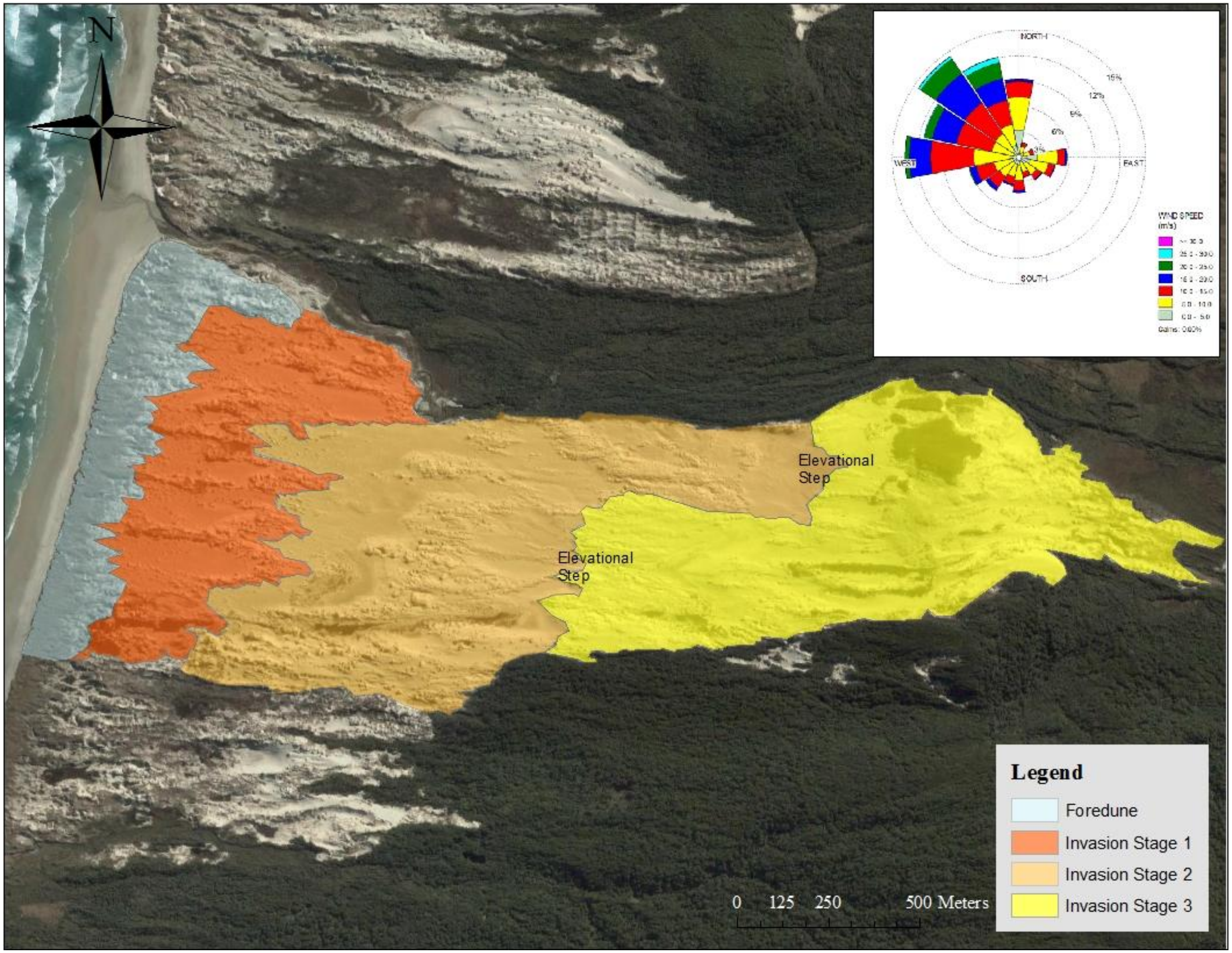

Figure 6.1: The conceptual model of invasion by marram grass seed into the central dune system at Mason Bay. In the model, four stages of marram grass invasion are shown and the elevational step is marked at the boundary between invasion stage 2 and invasion stage 3. The wind rose was developed from meteorological data collected at South West Cape, Stewart Island (Petersen, 2010). A discussion about the use of this data is presented in section 6.4.

6.3 Processes of invasion

6.3.1 Stage 1

Marram grass seed originates from the foredune on the western side of the central dune system at Mason Bay (Figure 6.1). This region can also be expanded to include the trailing arm and coppice dune populations of flowering marram grass, although seed crop size in these environments is much lower. Its position on the exposed, west-facing coast of Stewart Island makes Mason Bay particularly vulnerable to strong onshore nor-west to westerly winds (Figure 6.1), ideal for not only aeolian sediment transport but also the dispersal of seed.

The estimated seed crop size of the foredune complex, and trailing arms and coppice dunes of the adjacent parabolic dunes is 2,809, 197 and 39 seeds m^{-2} respectively (Chapter 2). When projected over the whole foredune and parabolic dune system, the seed production of the marram grass population in this region could equate to many hundreds of thousands of seeds, making the idea of seed dispersal into the central dune system seem much more viable. Following the discussion of those factors that are likely to increase seed production in marram grass (Chapter 2), it is no surprise that the greatest seed crop size in this region was found at the foredune face (7,691 m^{-2}). The description of the path for invasion in the following section will therefore begin at the foredune face, where seed production is highest.

Airflow velocities were measured for the foredune complex at Mason Bay by Petersen (2010) (Figure 6.2). The greatest horizontal airflow velocities occur between the crest and the middle of the foredune complex, followed by a steeply decreasing velocity gradient into the region of the backdune face. The model developed by Petersen (2010) also shows that airflows gain verticality up the stoss face of the foredune and accelerate after passing the foredune crest. This is similar to the process described by Arens (1996) who found that the foredune topography forced air into ‘jettation’ flows over the foredune crest. These flows may entrain seed from the flower spikes on the foredune face and jettison them vertically into the horizontal airflows above the foredune. Petersen (2010) also notes that greater vertical air velocities propel sand grains higher in the air, meaning more time for horizontal airflow velocities to transport sand inland before gravity effects deposition. Although sand grains are much lighter than marram grass seed, this same process may function on a smaller scale during seed dispersal.

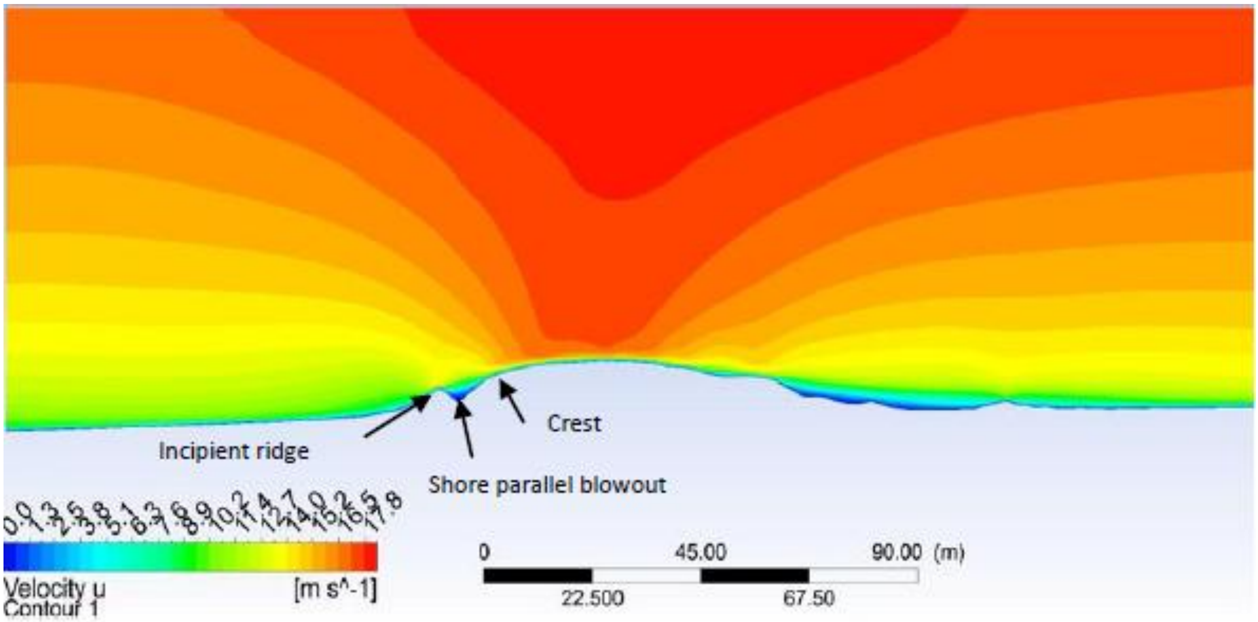

Figure 6.2: The modelled airflow velocity contours over the foredune complex at Mason Bay. *Source*: Petersen (2010).

Petersen (2010) noted that the episodes of greatest movement of sand were dependent on the number of days with strong transport-capable onshore winds and dry/warmer antecedent conditions. At Mason Bay, the highest occurrence of onshore north-westerly winds and dry conditions occurs between late spring and autumn. Under such transport-favourable conditions, it may be possible for marram grass seed to be lifted into the horizontal airstream and be deposited past the dense stands of marram grass on the foredune complex. This enables the secondary dispersal of seed in the relatively bare deflation surfaces and subsequent invasion into the dune hinterland. Although evidence for the distance travelled by wind dispersed seed is limited, Tackenburg (2003), during modelling of long distance dispersal in plant diaspores, found that rubber balloons, with a falling velocity of 0.9 m/s, could travel over 100m. Rubber balloons were considered to be representative replacements for *Cirsium arvense* (L.) pappi and *Senecio nemorensis* pappi (both have a falling velocity of 0.15 m/s) in release experiments used to validate Tackenburg's model. It was found that warm thermal conditions, which produced thermal turbulence and convective updrafts, were most important to long distance wind dispersal compared to horizontal wind speed (Tackenburg, 2003), which is often quoted as the key factor in determining dispersal distance (Soons *et al.*, 2004). Nathan *et al.* (2005) also suggest that turbulent wind flows of sufficient length and energy were required to lift seeds up high, thereby increasing dispersal distance. Besides Pope's (2005) investigation into secondary dispersal, no dispersal data is present for marram grass seed and therefore Tackenburg's findings are used as evidence for the potential of marram grass seed to disperse relatively long distances.

Therefore in the warm summer months at Mason Bay, which coincide with seed release, strong nor-westerly wind conditions may be capable of transporting seed past the foredune complex, especially in the foredune face where seeds may be more likely to be entrained. Another point in favour of dispersal of marram grass seed past the extent of the foredune complex is the sheer volume of seed that is produced in this population. As mentioned previously, on average, the foredune complex produces 2,809 seeds m^{-2}. This number, spread over the entire foredune complex, would equate to a large number of potentially viable seeds that could experience the right thermal and wind conditions ideal for transport into the central dune system.

Once seed has been carried past the foredune complex, it will most likely land in the deflation surfaces of the parabolic dunes. These are generally flat, stony surfaces interspersed with scattered coppice dunes, ideal for secondary dispersal of marram grass seed, due to the reduction in surface obstructions. Pope (2005) in his investigation of phase II dispersal at Mason Bay found that marram grass seed was highly mobile in light wind conditions. At wind speeds of 1 m/s, maximum dispersal distance was approximately 250 cm, whilst at 4 – 5 m/s the dispersal distance was approximately 1.5 m. This distance increased exponentially with increasing wind speed. At 7.1 m/s only one seed was recovered, trapped 20 m from the initial dispersal point by a piece of surface debris, which was considered by Pope to be a lucky find. Pope also noted that in terms of tracking marram grass seed, it became almost impossible to track in wind speeds of greater than 5 m/s due to the random nature of dispersal and the distances over which secondary dispersal occurs. This experimental issue was also shared by Tackenburg (2003) in similar release experiments, hence the use of rubber balloons. This highlights the potential for marram grass seed to travel great distances after phase I dispersal.

Once on the deflation surface, marram grass seed is thought to travel via secondary dispersal to the depositional lobes of the parabolic dunes, where it may settle, germinate and establish. The depositional lobes represent the maximum dispersal distance of stage 1 of the invasion process, when invasion begins from the foredune, coppice dunes and trailing arms. Of course some seeds may disperse beyond this point or within the boundaries of stage 1. However it is thought that given the distance between the depositional lobes and the foredune complex as well as the nature of the depositional lobes, where sand and by proxy seed is most likely deposited, this is an ideal environment for the end of stage 1 in the invasion process. Any seeds establishing within the boundaries of stage 1 will likely form their own coppice dune and add to the coppice dune population.

The time taken for marram grass seed to germinate, establish and mature into a flowering individual is not well known and therefore predictions made about this aspect of the invasion process will be less reliable. It is expected that once a seed germinates and establishes, it will start to form a small nabkha dune which will grow depending on sand supply and wind conditions (Wang *et al.*, 2006). Once this marram-induced nabkha has established and reached a certain size, it would be expected that the marram grass individual would flower and provide a new source of seed for invasion. At Mason Bay, observations suggest that marram grass seedlings form nabkha, mature and flower in 18 – 24 months and are approximately 1 m – 1.5 m in height (M. Hilton, Pers. Comm.). This observation is similar to Huiskes (1979) who stated that marram grass takes a minimum of two years from germination of seed for inflorescences to appear. It was thought therefore that the time taken for marram grass to mature and form nabkha was probably between two to three years.

6.3.2 Stage 2

By stage 2 of the invasion process, it is assumed that marram grass seed has dispersed from the foredune complex, trailing arms and coppice dunes to the depositional lobes and matured into flowering individuals. From here seed will be dispersed into the large central dune area where the secondary seedling distribution data (Chapter 4) shows over seven thousand seedlings were found during systematic surveys of this area over the course of five years. The boundaries of stage 2 were drawn somewhat arbitrarily due to a lack of observational and experimental evidence; however a pattern emerged with respect to seedling distribution that suggested specific boundaries to dispersal. In Figure 6.3, seedling distribution was concentrated along the northern and southern boundaries of stage 2 in the central dune system at Mason Bay. There also appears to be a strong concentration of seedlings along the western boundary of stage 2, in the stonefield and along the margins of the large wet depression. Unfortunately, no seedling surveys were conducted in the north-western corner of the large stonefield however, from observed seedling distribution patterns, this region was likely to contain many seedlings as well. There also appears to be some emergence of seedlings in stage 3 to the west of big sand hill. The reason for these concentrations is not known and is beyond the scope of this study to investigate, however drawing the boundary between stages 2 and 3 did inadvertently coincide with elevational steps (marked in Figure 6.1) in the central dune system which may have some explanation for this phenomenon. These concentrations provided ideal boundaries for stage 2 of the invasion process and differences in seedling concentration may suggest the presence of obstacles to dispersal, germination and establishment which were highlighted in Chapter 3.

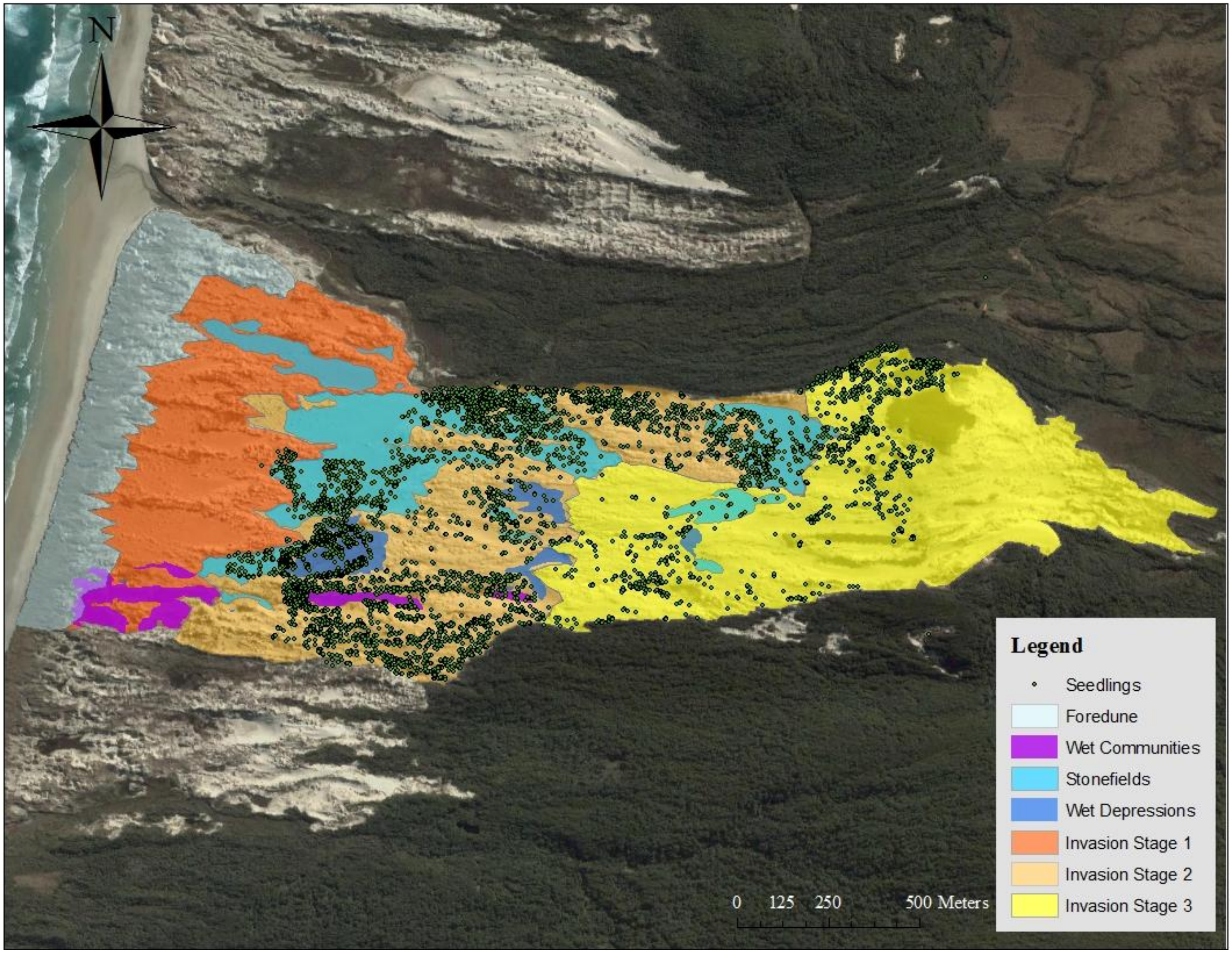

Figure 6.3: The conceptual model of invasion by marram grass seed in the central dune system of Mason Bay with the three stages of invasion, deflation surfaces and seedlings depicted.

6.3.3 Stage 3

After another period of two to three years, the marram grass seedlings of stage 2 will mature and form nabkha dunes (Figure 6.4). Once these seedlings have matured into flowering individuals, seeds may disperse further inland, up the elevational gradient, and into the backdune region of Mason Bay. Although no field investigations were carried out, observations by the author suggest that marram grass seedlings are less abundant in the dune region of stage 3 west of big sand hill. This may be related to unfavourable germination conditions, lack of burial in this region or barriers to dispersal caused by the elevational step. East of Big Sandhill however, there are larger established populations of marram grass on the sandsheets and the backdune nabkha which are characterised by vigorous flowering. This suggests that conditions in this area are ideal for the establishment of marram grass seedlings and the production of large volumes of seed. Although less frequent, the wind rose in Figure 6.1 highlights an easterly component to the wind regime at Mason Bay which may facilitate some dispersal of seed from this highly productive region back into the central dune system. Unfortunately this study was unable to quantify this phenomenon and can therefore only be considered as a possible vector for invasion.

Figure 6.4: Nabkha formation by marram grass in the northern dune system at Mason Bay. This is an example of the nabkha that may have formed in the central dune system. Unfortunately photographs of the nabkha in the central dune system were not available due to ongoing control operations which have resulted in the degradation of these landforms in the study area.

6.4 Model assumptions and future research

The prevailing idea, that seed ecology is relatively unimportant for marram grass dispersal (Huiskes, 1979; Hertling and Lubke, 1999; Krajnyk and Maun, 1982; Maun, 1984), has resulted in very little research being conducted on this topic. Consequently there are large gaps in our knowledge relating to phenomena such as the time taken for marram grass to establish and produce seed, potential seed dispersal distance and what factors are the most important for settlement and establishment, among others. Due to the incomplete understanding of marram grass seed ecology, the model developed during this study required several assumptions and should be viewed cautiously as a general process of invasion. Invasion of marram grass into different dune systems will vary depending on local site-specific factors such as wind velocity, wind direction and seed supply. This section will focus on the assumptions inherent in different aspects of the invasion model for Mason Bay including: 1) the potential dispersal distance achieved by seed; 2) the boundaries of each stage of invasion; 3) the proportion of seed surviving between stages; 4) the time taken for one generation to complete a full life cycle; 5) that flowering individuals in the sandsheet have a seed crop size between the minimum and maximum values found in Chapter 2; and 6) that the meteorological data collected from South West Cape is the same as that experienced at Mason Bay.

The first and potentially most important assumption for the dispersal model was the estimation of dispersal distance achieved by marram grass seed, which was represented by the three stages of invasion. Unfortunately, almost no empirical or anecdotal evidence was available relating to key questions such as average primary or secondary dispersal distance, maximum dispersal distance, or the proportion of seeds that disperses greater than a specific distance i.e. a dispersal curve. Estimations of dispersal in marram grass seed therefore were made from studies looking at dispersal distance in other plant diaspores (Nathan *et al*., 2005; Soons *et al*., 2004; Tackenburg, 2003) and from Pope's (2005) study. In the foredune population, the most common fate of seeds is likely to be dispersal only a short distance into the rank growth of the adult marram grass population of the foredune complex. This effectively halts secondary dispersal which was found by Pope (2005) to be the most effective method of seed dispersal in marram grass seed. Pope's (2005) findings of secondary dispersal distance in marram grass seed suggest that it may disperse extremely long distances given correct environmental conditions; especially when considering a significant percentage of winds at Mason Bay exceed 8 m/s. This made the development of invasive stages difficult in the model and informed estimations had to be used to delineate stage boundaries.

The first stage of the invasion model contained the foredune complex and parabolic dunes ending at the depositional lobes. It was assumed that these lobes were an ideal spot for seed settlement because of the propensity for sand, and by proxy seed, to be deposited on these features. This sand supply would also provide ideal conditions for marram grass seedlings to establish and mature into flowering individuals. The second stage was delineated based on trends observed in seedling distribution during analysis of the seedling survey data (Chapter 4). Figure 6.3 indicates that the majority of seedlings were concentrated within the area encompassed by stage two. Outside of this area, there appeared to be a fewer seedlings and it was therefore surmised that some factor may be responsible for slowing dispersal and establishment to the rest of the back dune system. Stage three, encompassing the remaining open sand dune environment at Mason Bay, consisted of a relatively steep elevational gradient extending up to approximately 60 m above sea level before reducing in height again eastward of Big Sandhill. Seed dispersing into stage three may therefore be sparse due to reduced seed rain and the elevation over which seed must disperse. Stage three could not be further divided into specific stages of invasion due to a lack of knowledge.

Another key question relating to the invasion process is what proportion of the seed rain actually establishes and matures into flowering individuals? This is currently unknown in any population of marram grass worldwide and would likely vary considerably between dune systems. The current conceptual model assumes that at least a small proportion of the seed crop would establish and mature in the central dune system at Mason Bay. Future research into this element of seed ecology would aid researchers and land managers in interpreting the likelihood of the processes described in the conceptual model.

In addition to understanding the proportion of the seed rain that establishes, it is also important to investigate the time taken for the invasion process to complete one generation. This information is primarily of importance to users who are controlling marram grass as it provides an estimation of project length. In the conceptual model developed in this study, it was assumed that marram grass seed requires between two to three years to establish and mature into flowering individuals. This is based on field observations made over the duration of control operations at Mason Bay (M. Hilton, Pers. Comm.). Further investigation into this aspect of seed ecology may however be required to garner a more accurate understanding of the time taken for the marram grass invasion process to take place.

Although this study estimated seed crop size of marram grass populations in each of the depositional environments, due to the length of control operations at Mason Bay, no data could be obtained for seed production of mature individuals in the sandsheets of the central dune system. Photographic evidence suggests that large mature individuals did exist here although these have largely been controlled and subsequently removed (Figure 6.5). The invasion model therefore assumed that seed production from mature individuals in the sandsheets of the central dune system, had a production between the minimum and maximum values of seed crop size estimated in Chapter 2 and that a proportion of this crop would disperse and establish in the next stage of invasion.

Figure 6.5: A flowering, mature individual in the sandsheet environment of the central dune system at Mason Bay which has been controlled. This highlights the presence of flowering individuals in the central dune system prior to control.

The final assumption is that the meteorological data collected at South West Cape, Stewart Island, for the development of the wind rose by Petersen (2010) accurately explains the wind regime at Mason Bay. The use of this meteorological data in the creation of the wind rose however was necessary as this was the closest climate station to the study site. This is not expected to greatly affect the creation of the conceptual invasion model because only a broad indication of wind regime was required. Figure 6.6 shows the spatial location of South West Cape compared to Mason Bay.

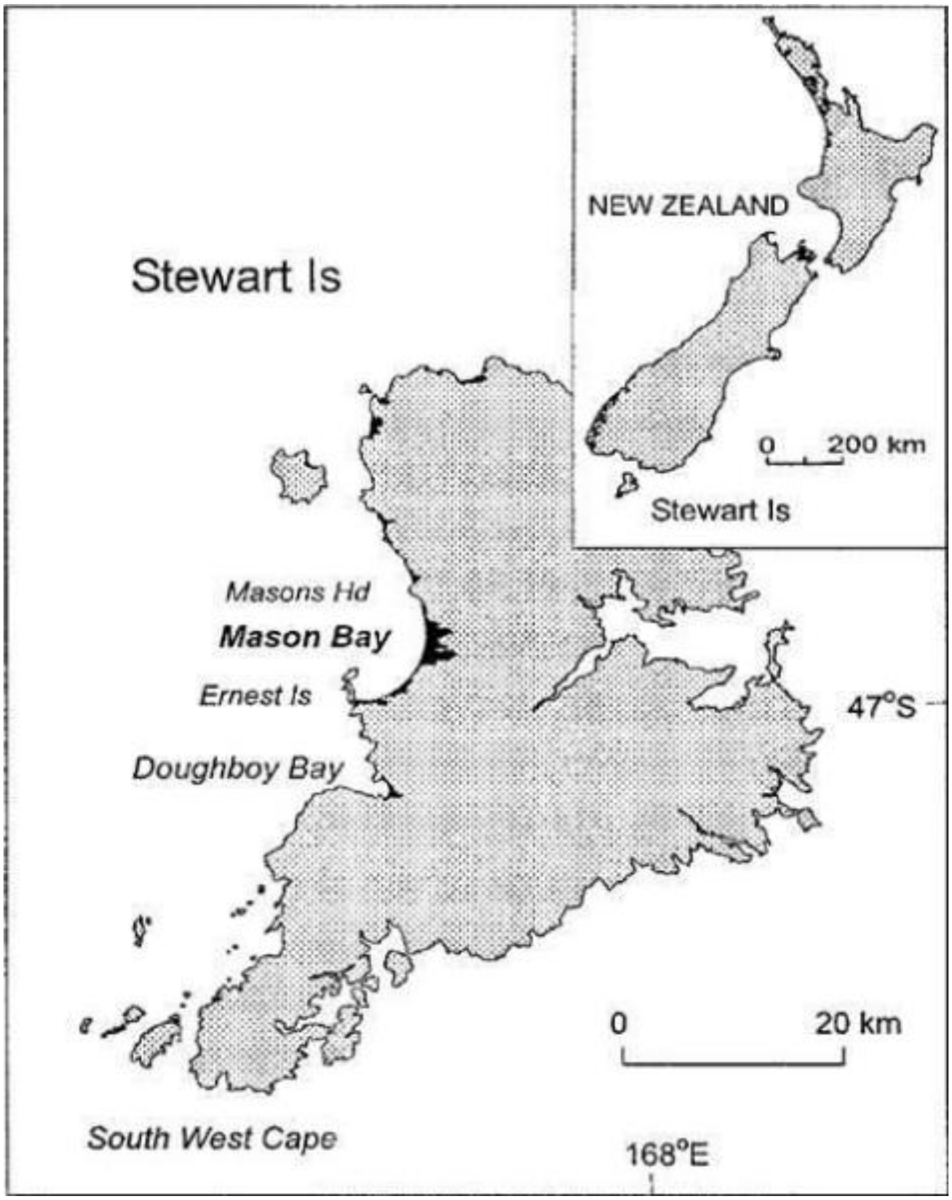

Figure 6.6: A map indicating the location of Mason Bay and South West Cape, Stewart Island. *Source*: Hilton et al., 2005.

6.5 Chapter summary

This study has shown clear evidence of marram grass invasion via seed. The development of a conceptual model of invasion by marram grass seed was a key outcome of the research and was based upon both the findings of this study and previous research relating to seed ecology. The conceptual model included four stages of invasion, with the origin of invasion based primarily in the foredune complex at Mason Bay. The process of invasion and the aspects of the model were discussed in section 6.3 and the assumptions associated with the conceptual model of invasion as well as directions for future research were discussed in section 6.4.

During discussion of the assumptions associated with the conceptual model, a number of areas for future research were highlighted. It is clear that more research into the general seed ecology of marram grass is required to properly understand an invasive species that threatens many of New Zealand’s nationally and internationally significant dune systems. These aspects of seed ecology include: 1) the actual and potential dispersal distances of marram grass seed; 2) the time taken for establishment and further invasion by marram grass; 3) the proportion of survival in dispersed seeds; and 4) seed production in environments where adult individuals have been removed i.e. the sandsheets.

The development of this conceptual model has highlighted the incomplete knowledge base of marram grass seed ecology. It also highlights to the reader the need to apply caution when interpreting the model, as there are many assumptions. With future research into marram grass seed ecology, there may be a greater degree of certainty to the development of conceptual models of invasion by marram grass which may better inform control operations of this invasive species.

Chapter 7

Summary and management recommendations

7.1 Introduction

The invasion of marram grass has had a significant impact on the biodiversity and landform diversity of southern New Zealand's dune systems (Hilton, 2006; Hilton *et al.*, 2005; Partridge, 1995). To date, the majority of research into marram grass invasion has focused on vegetative reproduction as the predominant mode of spread, with sexual reproduction being regarded as less important (Huiskes, 1979; Hertling and Lubke, 1999; Krajnyk and Maun, 1982; Maun, 1984). Recent empirical and observational evidence however suggests that seed ecology may play a much more important role in marram grass invasion than previously thought (Konlechner and Hilton, 2009). There is a relative paucity of experimental information relating to marram grass seed crop size, dispersal, dormancy, germination, the seed bank and the invasion process via seed. Of these topics, only seed dispersal and viability of seed have been studied in any detail in New Zealand (Pope, 2005). The current study therefore pursued four lines of enquiry relating to key aspects of marram grass seed ecology in order to further understanding of invasion via marram grass seed in southern New Zealand. The main findings of each of these lines of investigation are summarised in the following section.

7.2 Main findings

7.2.1 Chapter 2: Seed production at Mason Bay, Stewart Island

Chapter 2 aimed to estimate the seed crop size of flowering marram grass populations at Mason Bay and thus provide empirical data representing the potential for downwind seed transport in a southern New Zealand dune system. Seed crop size was calculated by measuring flowering density m^{-2} and quantifying the number florets per flower spike in six different depositional environments. Differences in estimated seed crop size were examined with respect to fresh sand supply and the vigour of the flowering populations of marram grass between six depositional environments including the northern nabkha, foredune complex, trailing arms, coppice dunes and backdune nabkha and sandsheets (Table 2.7). The foredune complex was further separated into three units, the foredune face, foredune mid-zone and backdune face for more comprehensive analysis of seed crop size in this depositional feature. The backdune nabkha were located in the backdune region east of Big Sandhill while the northern nabkha were located in the northern dune system at Mason Bay (Figure 2.2).

Estimation of seed crop size indicated that the northern and backdune nabkha had the highest potential seed crop size m^{-2} (17,383 and 17,772 respectively). The lowest potential seed crop size m^{-2} was found in the coppice dunes and trailing arms of the parabolic dunes (39.4 and 197 respectively). The foredune complex, which is likely the main source of seed invading into the central dune system, had an intermediate potential seed crop size of 2,809 seeds m^{-2}. However there was significant variation between the units of the foredune complex where the foredune face and foredune mid-zone had a high potential seed crop size of 7,691 and 2,155 seeds m^{-2} respectively and the backdune face had a low potential seed crop size of 243 seeds m^{-2}. These findings suggest that marram grass populations in environments with the highest inputs of fresh sand will flower the most vigorously and potentially produce the greatest amount of seed. When compared against the findings of other studies, seed crop size estimates at Mason Bay are generally similar to or higher than the estimates of other studies.

7.2.2 Chapter 3: Germination of marram grass seed

Chapter 3 investigated the germinability and viability of marram grass seed collected from a flowering population in southern New Zealand. The effects of light and darkness on the germination of marram grass seed as well as emergence of seedlings from burial were also investigated. Identifying those factors that affect germination and emergence in marram grass seed is an important aspect of objective one of the current study (Chapter 1). The findings of this aspect of the investigation were discussed with respect to light sensitivity in marram grass seed and the potential mechanisms behind this phenomenon.

Percent germinability of marram grass seed ranged between 28% and 94% depending on germination treatment. The relationship between percent germination and treatment suggests that under conditions of optimal water uptake, marram grass seed possesses high germinability of between 82% and 94%. When tested with tetrazolium chloride, percent viability of marram grass seed was 58%, which was similar to the findings of Pope (2005). The difference between this value and germinability of fresh seed indicates the loss of viability with increasing storage time.

Light treatments showed a greater rate of germination (68%) compared to dark treatments (33%), while dark treatments that were subsequently exposed to light for 21 days showed an increase in percent germination (70%). These results suggest that marram grass seed is highly sensitive to light which was attributed to two potential causes: 1) a strong, innate sensitivity to even weak green and red light possessed by marram grass seed; and/or 2) that seeds may have reacted to artificial and natural light exposure during preparation for germination in the dark. The exact mechanism behind the high light sensitivity could not be ascertained by the study, however these findings suggest that marram grass seed is well adapted to the constantly shifting substrate in the coastal dune environment which may result in rapid changes in burial.

Emergence in marram grass seed occurred at a maximum burial depth of 5 cm. The greatest percent emergence occurred in the 0.5 cm control treatment (29.33%) while the 5 cm treatment showed 4% emergence. Subsequent germinability and viability testing of recovered seed showed that although many seeds did not germinate and emerge, a large percentage remained viable during the 42 day burial period. Three causes were suggested for the results of seedling emergence including: 1) that seedling emergence was inhibited by the lack of a light stimulus; 2) that an inhibitor from the seeds' metabolism may have enforced dormancy in seeds; and/or 3) that compaction by the sediment surrounding the seed prevented the penetration of the radicle through the glumes. Taking into account the results of the investigation into the effects of light and darkness, it appeared that the prevention of light penetration by burial was the key cause for the inhibition of germination and emergence in marram grass seed.

7.2.3 Chapter 4: Seedling distribution

Seedling distribution was analysed using a combination of primary and secondary GPS data collected from Mason Bay. GPS point locations of seedlings were compared against marked deflation surfaces in order to determine where seedlings tended to establish. This line of enquiry also focused on objective one by identifying those dune environments which favour germination, emergence and the subsequent establishment of seedlings. This information compliments the findings of Chapters 2 and 3 and was used in the development of a conceptual model of marram grass invasion via seed.

The findings of this aspect of the study showed that there were fewer seedlings contained within the boundaries of the deflation surfaces (31.7%) compared to outside the deflation surfaces (68.3%). This finding contradicted literature which suggests that seeds will preferentially germinate and establish in wetter, sheltered environments compared to sandsheets (Fowler, 1986; Harper *et al.*, 1965; Huiskes, 1979; Laing, 1958; Winkel *et al.*, 1991). Within the deflation surfaces, the stonefields contained the greatest proportion of total seedlings (94.4%, n = 1150) but only because these surfaces were more widespread. Wet communities had the greatest seedling density, as could be expected based on previous studies, but due to their limited extent, did not contribute as much to the overall seedling population. The greater abundance of seedlings in the sandsheets at Mason Bay may have been due to three reasons: 1) seeds outside of deflation surfaces have a greater chance of burial; 2) the sandsheet environments are more extensive compared to deflation surfaces; and 3) the rainfall regime at Mason Bay makes conditions mesic enough to nullify any advantages that deflation surfaces possess over sandsheet environments. It may be that a combination of all three may explain the pattern of seedling distribution observed at Mason Bay.

7.2.4 Chapter 5: Seed bank longevity

The final line of investigation focused on objective two of the study by determining the nature and longevity of the marram grass seed bank in two southern New Zealand dune systems (Chapter 1). At both dune systems, novel methods of ageing the seed bank were employed which yielded a new understanding of the dynamics of marram grass seed banks. At St Kilda Beach, a 21 year dune profile record was used to age seeds sampled from the foredune ridge. At Allan's Beach, a set of aerial photographs and a Google Earth image dating back 28 years were used to reconstruct the development of four parallel dune ridges which enabled the ageing of the seed bank.

At St Kilda Beach, viable seed was aged between 0 – 21+ years old with the majority of seeds being aged between 0 – 8 years (82.8% germination), while seven seeds were aged 21+ years (71.4% germination). At Allan's Beach, viable seed was aged between 0 – 20 years, where the majority of seeds were obtained from dune ridges 2 and 3 (1 – 4 and 4 – 20 years old respectively), while no seeds were recovered from dune ridge 4. Germinability in dune ridges 2 and 3 were 94.7% and 85% respectively, while dune ridge 1 showed 66.7% germinability. The previous longest estimate of the marram grass seed bank was 'at least 9 years' (Konlechner and Hilton, 2009), making the findings of the current study particularly significant. These findings have important implications for current and future marram grass eradication programs and are used to form the management recommendations in section 7.3.

7.2.5 Chapter 6: The invasion process

The four lines of enquiry were synthesised into a conceptual model of marram grass invasion in the central dune system of Mason Bay and were a key outcome of the current study. This is the first conceptual model of invasion developed for marram grass seed dispersal and highlights the important role seed plays in marram grass invasion in large transgressive dune systems. It is hoped that this model can be used to inform future marram grass control operations and provide direction for future research which was highlighted in section 6.4.

The model was divided into four stages of invasion including: 1) the foredune, which is considered to be the main source of seed for invasion; 2) stage 1, the maximum distance over which seed is thought to initially disperse before settling and establishing; 3) stage 2, the next part of the dune system over which seed is estimated to potentially disperse and establish in; and 4) stage 3, the final part of the dune system, over which dispersal and establishment can occur. The stage boundaries were determined using both the findings of the current research and previous studies relating to: 1) how far seed is likely to travel; 2) natural barriers such as depositional lobes of the parabolic dunes and elevational steps; and 3) inferences taken from the analysis of seedling distribution patterns. The estimated time taken for marram grass to successfully invade the central dune system at Mason Bay was estimated to be between six and nine years based on observations of the time taken for a marram grass seedling to establish and flower in both New Zealand (M. Hilton, Pers. Comm.) and its home range (Huiskes, 1979). Discussion of the assumptions behind the development of the conceptual model also identified broad areas for future research which were: 1) the actual and potential dispersal distances of marram grass seed; 2) the time taken for the establishment of secondary populations and further invasion by marram grass seed; 3) the proportion of survival in dispersed seeds; and 4) seed production in environments where adult individuals have been removed i.e. the sandsheets.

7.3 Management recommendations

This study has focused on four key areas of marram grass seed ecology: 1) the estimated seed crop size of flowering populations of marram grass in different depositional environments; 2) the factors that affect germination of marram grass seed in the dune environment; 3) those areas in the central dune system which support a greater percentage of seedling emergence/establishment; and 4) the presence of a seed bank and its potential longevity in the dune systems of southern

New Zealand. The findings of this study have highlighted some important aspects of marram grass seed ecology which need to be incorporated into future marram grass control programs. Therefore recommendations for marram grass control operations, both generally and more specifically at Mason Bay, will be presented which take into account these new findings. These are summarised in Table 7.1.

The findings of Chapter's 3 and 4 suggest that a search effort focused on the deflation surfaces defined in this study would not be the most effective method. Analysis of seedling establishment in the central dune system of Mason Bay showed that a greater percentage of seedlings establish in the sandsheet environments outside the bounds of the deflation surfaces. Within the deflation surfaces, stonefields contained approximately 94% of all seedlings. With respect to the seedling survey procedure in the central dune region of Mason Bay, effort needs to be focused mainly on these expansive sandsheet and stonefield environments rather than the wet depressions and wet communities. The author would therefore recommend a comprehensive search of the central dune system at Mason Bay every two to three years to eliminate any new seedlings that may emerge from seed. This period between surveys may also have to be reduced to one or two years if significant sources of seed, similar to that of the foredune complex, exist in the backdune environment. At Mason Bay, control has been ongoing for approximately 10 years, resulting in the removal of most of the flowering individuals in the central dune region, making the foredune complex and the backdune nabkha the only really significant seed sources.

An area of Mason Bay, which to date has largely been neglected by control programs, is the region east of Big Sandhill. Although the predominant wind regime is westerly, there is still an easterly component (see Figure 6.1). These winds, coupled with a large seed crop size in the populations of marram grass on the backdune nabkha (17,772 seeds m^{-2}), presents a second large source of seeds which may potentially disperse into the central dune system. This marram grass population should be eradicated to eliminate this threat of re-invasion. Experience from previous control operations suggest that any program undertaken in this region will take several years to achieve complete dieback (Main, 2008), however monitoring will need to be maintained to prevent re-invasion. Unfortunately the nature and longevity of the seed bank was not investigated in the backdune nabkha. However, the supply of fresh sand and vigorously flowering populations of marram grass suggest the potential for seed bank formation. Therefore search efforts should be focused on controlled nabkha in order to eliminate any new seedlings that may emerge and establish in this depositional environment.

A key finding of the current study was that the marram grass seed bank can remain dormant in the foredune up to and potentially beyond 21 years of age. This is particularly significant because marram grass seed may in fact play a very important role in the process of invasion. A long-lived seed bank represents a very serious threat of re-invasion back into previously controlled areas (Rao, 2000; van der Hagen *et al.*, 2008). To combat this phenomenon, a comprehensive monitoring program is required to prevent the re-establishment of ecologically significant populations, particularly in the foredune complex where ongoing progradation and aggradation is ideal for seed bank formation. The exact length of monitoring programs after control has never explicitly been defined for marram grass. The results of this study suggest that monitoring needs to occur for at least 21 years after control to eliminate any new seedlings originating from dormant seed. Seeds collected from St Kilda in 1965 still showed a germination response 45 years later however these failed to develop into healthy seedlings. This suggests that long-term marram grass seed viability is most likely at least 21 but less than 45 years. The post-control monitoring program therefore should involve a comprehensive search and removal of all seedlings in the foredune region every two years for a period of up to 45 years to prevent the establishment and maturing of seedlings into flowering individuals.

Table 7.1: A summary of the management recommendations for ongoing and future marram grass eradication operations.

Study finding	**Management recommendation**
1. A greater proportion of seedlings emerge/establish outside of deflation surfaces at Mason Bay. Of those found within deflation surfaces, the majority establish in stonefields.	Seedling survey effort should be focused on sandsheets and stonefields. A comprehensive search of the central dune system should be carried out every 2 – 3 years. This should be shortened to 1 – 2 years if there are significant seed sources in the central dune system.
2. The backdune nabkha population of flowering marram grass east of Big Sandhill has the second highest seed crop size at Mason Bay and is therefore a significant source of seed for re-invasion into the central dune system.	Undertake marram grass eradication operations in this region. Post-control monitoring will also need to be carried out here to prevent re-establishment. Search effort should be focused on controlled backdune nabkha in order to eliminate seedlings potentially originating from a seed bank.
3. Viable seed from the marram grass seed bank was aged between 0 – 21+ years old.	Following eradication of the flowering population on the foredune, the foredune should be checked for seedlings every 2 years for a period between 21 – 45 years.

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Appendix A

Table A.1: The dimensions and number of seed heads of the sampled nabkha from the northern nabkha depositional environment.

Nabhka	Height (m)		Width (m)	Length (m)	Area (m^2)	Volume (m^3)	Number of seed heads
	Nabkha	Marram					
1	0.5	0.8	2	1.6	3.2	1.6	240
2	0.45	0.85	1.6	0.9	1.44	0.648	153
3	0.5	0.9	2.16	1.46	3.15	1.58	480
4	2.2	0.8	6.1	4.2	25.62	56.36	600
5	0.4	0.95	1.8	0.8	1.44	0.576	266
6	1.2	1	2.5	2.1	5.25	6.3	259
7	2.3	0.8	4.8	3.35	16.08	36.98	1,620
8	0.8	1	2	0.7	1.4	1.12	77
9	0.25	0.95	1.3	0.85	1.11	0.28	45
10	0.55	0.8	2.1	0.5	1.05	0.58	193
11	0.5	1.25	2.4	1.55	3.72	1.86	628
12	1.1	1.2	3	1.2	3.6	3.96	502
13	0.15	1.3	1.9	1	1.9	0.29	164
14	0.9	0.7	0.85	0.6	0.51	0.46	4
15	1.3	1.15	3	2	6	7.8	558
16	1	1	3.65	4.25	15.51	15.51	360
17	0.85	1.1	2.5	0.65	1.63	1.38	276
18	0.3	1	1	0.3	0.3	0.09	69
19	1.9	0.9	8.2	3.2	26.24	49.86	2,614

Appendix B

Table B.1: Core A1 taken from St Kilda Beach on August 20th 2010 showing the number of sub-samples contained within the core and their corresponding depths. Coring began at 49cm in core A1 for reasons explained in section 5.3.2.

Core	**Start depth (cm)**	**End depth (cm)**	**Depth range (cm)**	**Core size (cm)**	**Notes**
A1	49	63	49-63	14	
A2	63	77	63-77	14	
A3	77	88.5	77-88.5	11.5	
A4	88.5	99	88.5-99	10.5	
A5	99	117	99-117	18	
A6	117	131	117-131	14	
A7	131	143	131-143	12	
A8	143	154	143-154	11	
A9	154	167	154-167	13	
A10	167	179	167-179	12	
A11	179	198.5	179-198.5	19.5	
A12	198.5	212	198.5-212	13.5	
A13	212	221	212-221	9	
A14	221	233	221-233	12	
A15	233	242	233-242	9	
A16	242	252	242-252	10	
A17	252	262	252-262	10	
A18	262	274	262-274	12	
A19	274	282	274-282	8	
A20	282	291.5	282-291.5	9.5	
A21	291.5	303	291.5-303	11.5	
A22	303	315	303-315	12	
A23	315	324.5	315-324.5	9.5	
A24	324.5	334	324.5-334	9.5	
A25	334	343	334-343	9	
A26	343	352.5	343-352.5	9.5	
A27	352.5	364.5	352.5-364.5	12	
A28	364.5	374	364.5-374	9.5	
A29	374	384.5	374-384.5	10.5	
A30	384.5	395	384.5-395	10.5	
A31	395	405.5	395-405.5	10.5	
A32	405.5	414	405.5-414	8.5	
A33	414	425	414-425	11	

Table B.2: Core A2 taken from St Kilda Beach on September 15th 2010 showing the number of sub-samples contained within the core and their corresponding depths.

Core	Start depth (cm)	End depth (cm)	Depth range (cm)	Core size (cm)	Notes
A2-1	0	42	0-42	42	
A2-2	42	66	42-66	24	
A2-3	66	81	66-81	15	
A2-4	81	101	81-101	20	
A2-5	101	123	101-123	22	
A2-6	123	143	123-143	20	
A2-7	143	161	143-161	18	
A2-8	161	185	161-185	24	
A2-9	185	197	185-197	12	
A2-10	197	209	197-209	12	
A2-11	209	215	209-215	6	
A2-12	215	230	215-230	15	
A2-13	230	240	230-240	10	
A2-14	240	251	240-251	11	
A2-15	251	260	251-260	9	
A2-16	260	267	260-267	7	
A2-17	267	276	267-276	9	
A2-18	276	286	276-286	10	
A2-19	286	300	286-300	14	
A2-20	300	309	300-309	9	
A2-21	309	318	309-318	9	
A2-22	318	322	318-322	4	
A2-23	322	335	322-335	13	
A2-24	335	345	335-345	10	
A2-25	345	357	345-357	12	
A2-26	357	369	357-369	12	
A2-27	369	379	369-379	10	
A2-28	379	390	379-390	11	
A2-29	390	401	390-401	11	
A2-30	401	413	401-413	12	

Table B.3: Core B taken from St Kilda Beach on September 15th 2010 showing the number of sub-samples contained within the core and their corresponding depths.

Core	Start depth (cm)	End depth (cm)	Depth range (cm)	Core size (cm)	Notes
B1	0	40	0-40	40	
B2	40	65	40-65	25	
B3	65	81	65-81	16	
B4	81	90	81-90	9	
B5	90	100	90-100	10	
B6					Labelling Error
B7	100	116	100-116	16	
B8	116	135	116-135	19	
B9	135	163	135-163	28	
B10	163	179	163-179	16	
B11	179	200	179-200	21	
B12	200	210	200-210	10	
B13	210	221	210-221	11	
B14	221	234	221-234	13	
B15	234	242	234-242	8	
B16	242	254	242-254	12	
B17	254	265	254-265	11	
B18	265	275	265-275	10	
B19	275	282	275-282	7	
B20	282	296	282-296	14	
B21	296	303	296-303	7	
B22	303	314	303-314	11	
B23	314	325	314-325	11	
B24	325	339	325-339	14	
B25	339	350	339-350	11	
B26	350	360	350-360	10	
B27	360	370	360-370	10	
B28	370	380	370-380	10	
B29	380	390	380-390	10	
B30	390	400	390-400	10	
B31	400	416	400-416	16	Small amount of sand fell in

Table B.4: A summary of the total number of sub-samples, total depth and location of the three cores taken at St Kilda Beach.

Core	**Total number of sub-samples**	**Total depth of core (m)**	**Core location**
A1	33	4.25	Point 1, 2m north
A2	31	4.16	Point 1, 2m south
B	30	4.13	Point 2, 2m north

Appendix C

A worked example of the seeds per 10 m^3 in core A1, St Kilda:

To calculate the volume of sand collected per core:

Area of corer = πr^2 = 314.16 cm^2

Depth of core A1 = 425 cm

Volume of core A1 = 314.16 x 425 = 133,518 cm^3

Volume of core A1 in m^3 = 133,518/1000 = 133.52 m^3 (2 d.p.)

To calculate the number of seeds per 10 m^3:

38/133.52m^3 = 0.285 seeds per m^3

0.285 x 10 = 2.85 seeds per 10 m^3

Therefore there are approximately 3 seeds per 10 m^3 of foredune at St Kilda