

SEED AND MICROSITE LIMITATION IN *CLEMATIS VITALBA*  
ON BANKS PENINSULA

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## ABSTRACT

*Clematis vitalba*, introduced to New Zealand from Europe in the early 1900s, is an invasive weed which poses a high risk to native forest remnants, particularly in the central North Island and upper and central South Island. Its dispersal techniques and rate of spread make it a particular challenge for managers attempting to control its range expansion. Is the population abundance and distribution of *C. vitalba* on Banks Peninsula seed or microsite limited? I tested the presence of seed limitation in three populations of *C. vitalba* at two sites by measuring seed dispersal and checking for the presence of a soil seed bank. At a location where *C. vitalba* is absent due to control efforts, I investigated the presence of a long-term seed bank and long-distance dispersal. I also tested the degree of microsite limitation in *C. vitalba* at the two sites by surveying the natural distribution of seedlings, monitoring seedling emergence after seed addition and measuring the survival and growth of planted seedlings. Soil samples taken from the Port Hills and Akaroa sites contained low amounts of previous-season *C. vitalba* seed (an average of 0.0125 seeds per m<sup>2</sup> in the forest and 0.0025 per m<sup>2</sup> in the open) and confirmed the presence of a small short-term soil seed bank. Seed rain was greater at Akaroa (3912 seeds caught) than on the Port Hills (1507 seeds caught), which is also reflected in a larger seed bank at Akaroa. The distribution of natural seedlings and growth of planted seedlings suggests that the optimum habitat for this species varies among different life stages. At the site cleared of *C. vitalba* more than eight years ago, there were no seeds in the seed bank but new seeds arrived by long-distance dispersal. Overall, these results suggest that microsite limitation has a greater role near the parent plant and seed limitation becomes more pronounced at increasing distance from the seed source. *Clematis vitalba* populations continue to spread from ongoing long-distance dispersal and short-distance dispersal with lateral expansion of established populations; established populations are more likely to be limited by the availability of microsites while expanding populations will be seed limited at the edge of the population where plant density is low.

## **CHAPTER 1 - Introduction**

### **1.1 Plant invasions in New Zealand**

Facilitated by a temperate climate, a lack of significant native herbivores and predators, and expanding areas of human-transformed habitat, introduced species have invaded New Zealand in a manner that is rarely equaled anywhere else in the world (Lee et al., 2006). Over half of all wild plant species in New Zealand are exotic species; the indigenous vascular flora contains about 2150 species and more than 2300 exotic species have been described as ‘naturalised’ or ‘casual’ (Howell, 2008). Approximately 19% of these naturalised species are currently listed as environmental weeds, species managed as weeds in conservation land by the New Zealand Department of Conservation (DOC) and/or New Zealand’s regional councils (Sullivan et al., 2009). Three-quarters of New Zealand’s current environmental weeds are “nice plants turned nasty”; species that were deliberately introduced for ornamental or horticultural purposes (Sullivan et al., 2005; Timmins and Blood, 2003).

### **1.2 The invasion of introduced plants: concepts and definitions**

The expanding field of invasion ecology has seen a proliferation of terms to describe various concepts, and there is considerable confusion of existing terminology (Richardson et al., 2000). For example, there is a lack of clarity and consistency in the use of the term ‘naturalised’ (Richardson et al., 2000). In the literature, what is described as colonisation may also be naturalisation, and a description of naturalisation may also correspond to the definition of invasive. One of the key tasks of invasion ecology is to explain why some species are better invaders than others, and this is greatly complicated if the criteria for judging success are poorly defined. Richardson et al. (2000) proposed the simple conceptualisation of the invasion process as shown in Fig. 1.1. Following this proposal, the process of invasion requires a plant species to overcome various abiotic and

biotic barriers. Introduction means that the plant has overcome a major geographical barrier. Many introduced species may survive as casuals; such species sexually reproduce but fail to maintain their populations over longer periods of time. Naturalisation begins when environmental barriers do not prevent individuals from surviving and when reproductive barriers are overcome and offspring recruit freely. At this stage, populations are sufficiently large that the probability of extinction due to environmental stochasticity is low. Invasion requires that the introduced species overcomes barriers to dispersal within the new region and can cope with abiotic and biotic factors it encounters there. The shift of a plant species from a naturalised non-native to an invasive represents the point where an introduced species starts to have detectable, detrimental ecological or economical consequences.

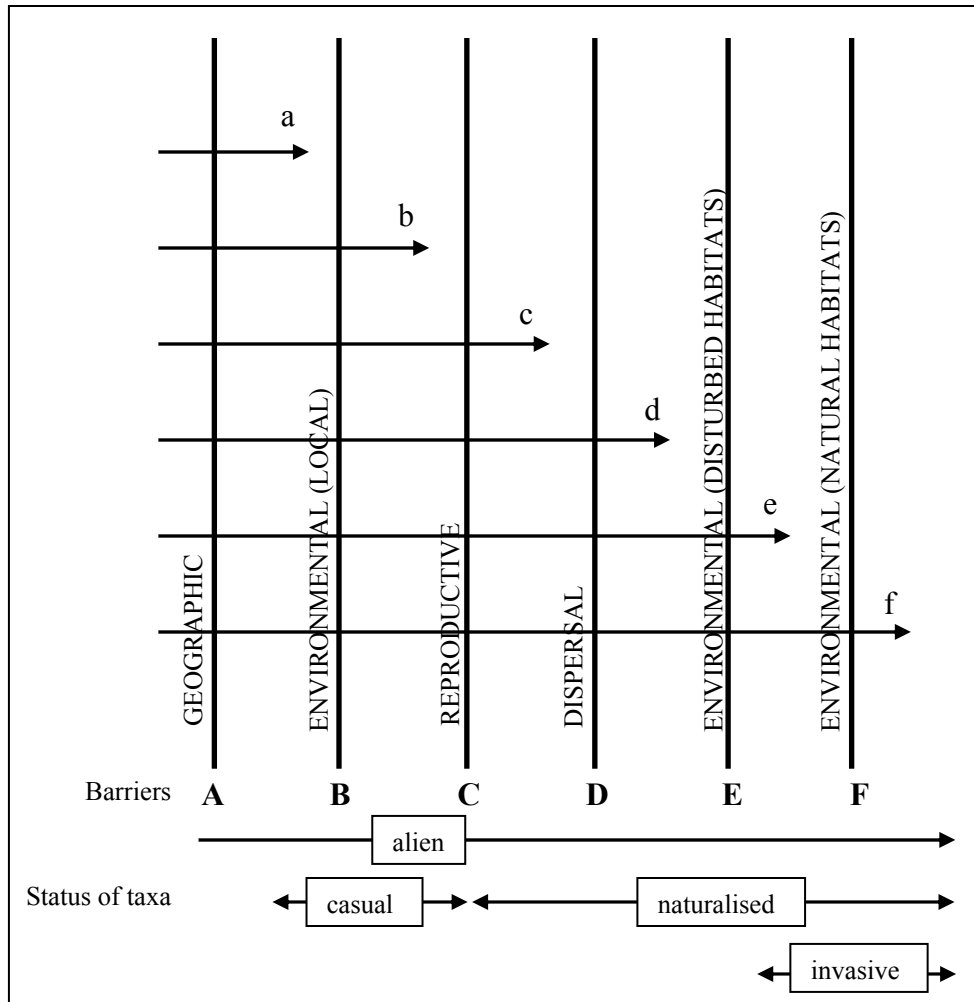


Fig. 1.1 A schematic representation of the major barriers limiting the spread of introduced species (Richardson et al., 2000). The barriers are: (A) major geographical barrier; (B) environmental barrier at the site of introduction; (C) reproductive barriers; (D) local/regional dispersal barriers; (E) environmental barriers in human-modified or alien-dominated vegetation; and (F) environmental barriers in natural or semi-natural vegetation. The arrows of a through to f illustrate the paths followed by a plant species to reach the different stages from introduced to invasive in natural vegetation.



### **1.3 Population recruitment in invasive species**

The successful invasion of environmental weeds has been correlated with traits such as dispersal and prolific seed production, however, site-specific factors will also determine invasion success (McAlpine and Jesson, 2008). Population recruitment in plants is primarily determined by two constraints: the availability of environmentally suitable sites (microsites) and the likelihood of seeds reaching those sites (Clark et al., 2007; Duncan et al., 2009; Moore and Elmendorf, 2006). These two constraints are known as microsite limitation and seed limitation respectively. They have received much attention in recent literature (for microsite limitation see Gómez-Aparicio, 2008; McAlpine and Jesson, 2008, for seed limitation see Clark et al., 2007; Jongejans et al., 2007; Turnbull et al., 2000 and for a comparison of both see Dalling et al., 1998; Duncan et al., 2009; Eriksson and Ehrlén, 1992). In the past, these two constraints have been studied independently and their occurrence in plant populations and communities debated. However, other studies, for example Turnbull et al., 2000; Zobel et al., 2000, illustrate that at issue is not which is present in a population but the relative importance of each.

#### **1.3.1 Seed limitation**

Seed dispersal is a critically important process in plant population dynamics, but it is almost never completely successful because seeds do not arrive at all suitable sites (Muller-Landau et al., 2002). The total number of seeds available for dispersal, determined by a population's adult abundance and fecundity, places an upper limit on the number of sites that can possibly be reached by seeds (Muller-Landau et al., 2002). Weed species are well-adapted for the efficient dispersal of their seed and dispersal by any vector, which results in widespread and prolific seed-deposition, and thus enhancing the chances of invasion success (McAlpine and Jesson, 2008).

Populations that are seed limited have fewer individuals than possible because the rate of seed supply is low relative to the number of available microsites (Clark et al., 2007;

Duncan et al., 2009). Seed limitation, also known as propagule limitation (Moore and Elmendorf, 2006), can be separated into two processes – source limitation and dispersal limitation. Source limitation occurs when there are not enough seeds produced to saturate potential recruitment sites even if seeds could reach all sites (Clark et al., 2007) - population size is limited by seed availability at the local scale (Münzbergová and Herben, 2005). Dispersal limitation occurs when seed dispersal is constrained and not all potential recruitment sites are reached, even though enough seeds are produced to fully saturate all sites (Clark et al., 2007; Muller-Landau et al., 2002). At a regional scale, the distribution of a species is limited by seed dispersal (Münzbergová and Herben, 2005).

### **1.3.2 Microsite limitation**

Microsite limitation, also known as establishment limitation (Clark et al., 2007), microhabitat limitation (Kollman et al., 2007) and niche limitation (Moore and Elmendorf, 2006), occurs when plant population size is constrained by the number and quality of available sites for establishment (Clark et al., 2007). At a local scale, population size is constrained by the availability of opportunities for establishment and growth, and at a regional scale, the distribution of a species is limited by the availability of suitable habitats (Münzbergová and Herben, 2005). Microsite limitation can be partitioned into several processes that occur between seed deposition and recruitment into the adult population, such as seed germination and seedling recruitment (Clark et al., 1998).

The availability of suitable microsites on a soil surface regulates the number of plants establishing from seed and thus the abundance of a species is determined (Harper et al., 1965b). A microsite, or a safe site, is a zone in which a seed may find itself which provides the stimuli required for breakage of seed dormancy, the conditions and resources needed for germination (Harper, 1977). The interactions of seeds with their environments determine seedling establishment patterns and influence the structure of both plant populations and communities (Chambers, 1995). The characteristics of the

microsite at which the seed arrives determines the probabilities of seed survival, germination and seedling emergence and survival (Chambers, 1995).

### **1.3.3 A continuum of limitation**

Seed limitation and establishment limitation are not mutually exclusive, but rather represent extremes of a continuum (Moore and Elmendorf, 2006). At one extreme, seeds disperse to all sites, but only establish where niche requirements are met (Duncan et al., 2009; Moore and Elmendorf, 2006). At the other, population distributions are wholly influenced by seed availability (Duncan et al., 2009; Moore and Elmendorf, 2006). If establishment limitation is predominant within a population, then abundance and distribution are restricted by competitive ability, regeneration niches, and the abundance and quality of microsites (Clark et al., 2007). If seed limitation is predominant, then the abundance and distribution of a species are better viewed in the context of a lottery system, where few sites are “won” by the best possible competitor and most are won “by default” (Clark et al., 2007). Recruits are drawn at random from the seeds that happen to arrive at the site (Clark et al., 2007).

## **1.4 Introduction to the species *Clematis vitalba***

The genus *Clematis* is a member of the family Ranunculaceae; the genus originates in Western Europe and contains about 300 species of vines and perennial herbs found throughout the world (Sawyer and Inman, 2006; Webb et al., 1990). There are nine species of *Clematis* endemic to New Zealand, including *C. paniculata* and *C. forsteri* (Sawyer and Inman, 2006). Webb et al. (1988) recognize five species of *Clematis* which are naturalised in New Zealand, including the popular garden plants *C. montana*, *C. flammula*, and *C. tangutica*, and the highly invasive *C. vitalba*. *Clematis vitalba*, also known as old man’s beard, is native to Europe (Webb et al., 1988) and its naturalised

range includes Ireland and Scotland, Poland, Denmark, north and north-eastern America, south Australia and New Zealand.

### **1.5 *Clematis vitalba* in New Zealand**

*C. vitalba* was introduced into New Zealand as an ornamental garden plant before 1922 (Gourlay et al., 1999) and naturalised between 1922 and 1935 (Ogle et al., 2000). The initial phase of naturalisation was lengthy (West, 1992). In the early 1940s, *C. vitalba* was initially recorded in Christchurch, was recognized as an escape from cultivation and had established mainly in waste sites and riverbanks (West, 1992).

In the 1950s, southern expansion along the Clutha River and south of Christchurch and expansion along the east coast of the North Island became evident (West, 1992). In the 1970s, *C. vitalba* was recorded on Stewart Island and the Chatham Islands, and as far north as Auckland (West, 1992). A large increase in abundance occurred in the 1980s; it was at this time that *C. vitalba* was first recognized as a serious weed and control of the vine began (West, 1992).

*Clematis vitalba* is now classified as a containment plant in the Regional Pest Management Strategy (RPMS) under the 'Biodiversity Pests' section and is under active control aimed at ensuring the species does not increase its range (Parks and Schmechel, 2009). It is also listed on the National Pest Plant Accord, an agreement between the Nursery and Garden Industry Association, the regional councils and government departments with biosecurity responsibilities (Roy et al., 2004). Under the Accord, regional councils will undertake surveillance to prevent the commercial sale and/or distribution of an agreed list of pest plants, which are also declared as unwanted organisms (Roy et al., 2004).

*Clematis vitalba* is now found throughout the country from north of Auckland to Stewart Island in the far south, grows well on a wide range of sites, and is commonly found in

towns and distributed along river systems and shelterbelts (Greer and Sheppard, 1990; Hume et al., 1995). It occurs in scattered populations on Banks Peninsula, particularly at Governors Bay, Akaroa, and on the Port Hills in Sugarloaf Reserve, Reuters Reserve, Otahuna and Barnett Park (Parks and Schmechel, 2009). Other occurrences in Canterbury include along the Ashley River, Waihi River, Hurunui River, Selwyn River, in Peel Forest and Kowai Bush.

### **1.6 Ecology of *Clematis vitalba***

The seedlings of *C. vitalba* are small rosette plants (Fig. 1.2 A) which mature into woody vines which can grow to heights of up to 30 m (Roy et al., 2004). The vine is deciduous and its juvenile leaves have three leaflets and the adult leaves have five leaflets (Fig. 1.2 A and B). The climbing strategy of the vine relies on other plants; leaflet petioles twine around saplings or shrubs (Baars et al., 1998; Roy et al., 2004). Twining stems successfully resist slipping or breaking under the weight of the main vine (Baars et al., 1998). The growth rate of *C. vitalba* is very high; stems can grow up to four metres during a single growing season and have an estimated productivity of  $6.3\text{kg/m}^2$  (Stein, 2004). This can be compared to the productivity of a tropical rainforest of  $4\text{kg/m}^2$  or an average New Zealand sub-tropical forest of  $1.2\text{kg/m}^2$  (Stein, 2004).

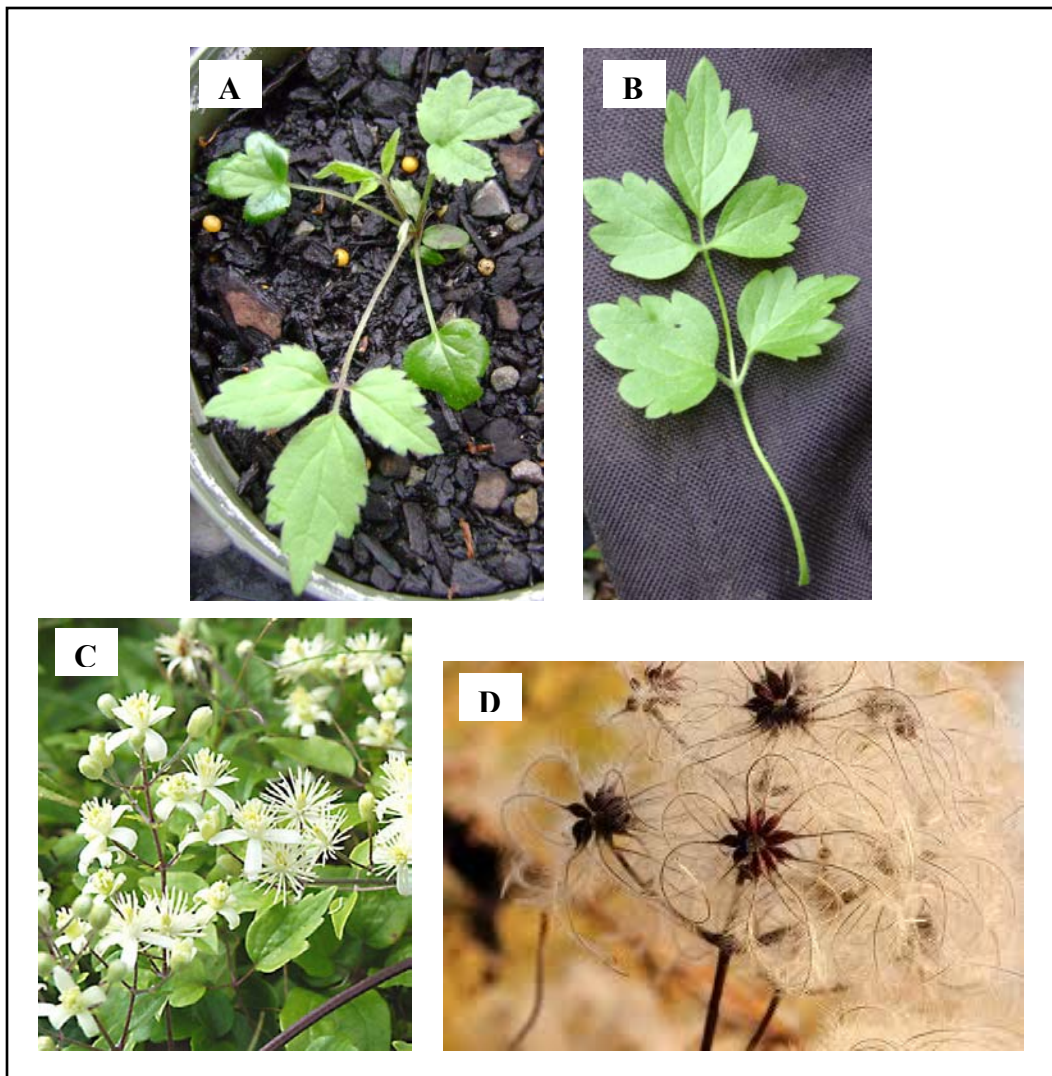


Fig. 1.2 Different growth forms of *Clematis vitalba*. A = a small seedling, height of approximately 5 cm. B = adult leaf, approximately 8 cm in length. C = inflorescence. D = mature seed heads, note the feathery tail which assists wind dispersal.

*Clematis vitalba* has creamy white flowers that are approximately 2-3 cm wide with hairy sepals bent back from a central cluster of stamens (Fig. 1.2 C) (Sawyer and Inman, 2006). The vines flower from December through to March or April in some areas, with the onset of seed from March onwards (Stein, 2004). The flowers are hermaphrodite, pollinated by wind and a variety of insects such as native syrphid flies, bees and butterflies (Sawyer and Inman, 2006; Stein, 2004). The flowers grow in tight bunches and little movement is required to distribute pollen amongst the bunches (Stein, 2004). Flowers are produced

only when the plant is growing in a position of high light; flowering can occur within one year of germination if conditions are favourable (Stein, 2004; West, 1992). The seeds are brown in colour, approximately 5 mm in length, and have a feathery style (Fig. 1.2 D) (Stein, 2004). The seed can lie dormant after dispersal but there has been no conclusive research into how long the seed can remain viable in the soil (Stein, 2004). Dispersal by seed is the primary means of distribution for this species, however, it can also spread by stem fragments or vegetatively - stems root when they touch the ground (Bungard et al., 1997a; Roy et al., 2004). As *C. vitalba* is self-fertile, one isolated vine can establish a new population (Stein, 2004).

*Clematis vitalba* has a 75% survival rate at a relative irradiance (RI) level of 2% (Baars and Kelly, 1996). It has a light compensation point close to 1% RI, which makes survival under an established canopy possible (Baars and Kelly, 1996). *Clematis vitalba* shows a rapid increase in stem length between 2% and 3.5% RI levels (Baars and Kelly, 1996). This growth response shows its competitive superiority in terms of its ability to increase biomass at low irradiance levels, allowing it to colonize low irradiance environments faster (Baars and Kelly, 1996). It displays rapid stem elongation at relatively low levels of irradiance which is an advantage where canopy gaps are small, as this enables the vine to reach the canopy before the gap closes (Baars and Kelly, 1996).

### **1.6.1 Factors affecting distribution**

In New Zealand, *C. vitalba* is a lowland plant and rarely found above 750 m (Atkinson, 1984). Sites free from browsing animals are necessary for seedlings to establish, as well as sufficient water to allow for rapid development over spring and summer (Stein, 2004). Most occurrences of this species are within the 800-1600 mm rainfall zone but in lower rainfall areas, gullies, seepages or other moist sites provide sufficient moisture to allow the establishment of the vine (Atkinson, 1984). In England, *C. vitalba* is most abundant on alkaline soils, but in New Zealand grows in soils of a wider pH range (Baars et al., 1998). Hume et al. (1995) found that *C. vitalba* is not restricted to soils of a high pH (the

range of soil pH recorded in their field soil samples was 5.0 – 7.6) and they found that it can grow well at a relatively low pH value of 4.7 with the death of plants occurring at a pH of 3.7.

Sites with *C. vitalba* in New Zealand differ in parent materials, but most are recent in origin with a high base saturation indicating high fertility (West, 1992). The species grows on a variety of soils; those which are rich in bases of calcium, potassium, magnesium and sodium (Atkinson, 1984). The absence of *C. vitalba* on heavy clay soils north of Auckland suggests that the physical and/or chemical conditions of these soils may restrict the growth of this vine (Atkinson, 1984). *Clematis vitalba* is often associated with riverbeds; waterways provide rapid seed dispersal (Stein, 2004) and alluvial soils often have high fertility (Atkinson, 1984; West, 1992). The growth of the vine may be restricted by very low concentrations of nitrogen, phosphorus, calcium and sulfur in the soil (Hume et al., 1995).

Rapid germination and vigorous growth in high-irradiance, high-N sites are key factors for the successful establishment of *C. vitalba* in forest gaps and margins (Bungard et al., 1998). Soil disturbance and the associated vegetation removal increase the rate of soil mineralization and reduce the uptake of nutrients by plants (Bungard et al., 1998). This can increase the amount of plant available N. *Clematis vitalba* has a light compensation point of about 0.9% RI (relative irradiance) and has the ability to increase biomass at low irradiance levels (Baars and Kelly, 1996). This allows it to colonize low irradiance environments faster and increase its chances of encountering more favourable habitats for growth (Baars and Kelly, 1996).

## **1.7 Research aims**

This study aims to test the hypothesis that the distribution and abundance of *C. vitalba* on Banks Peninsula is limited by a combination of seed dispersal and factors affecting establishment. Specifically, this study aims to investigate the relative importance of seed



limitation and microsite limitation in the spread of this species. The outline of this thesis is as follows:

- 1) Chapter 2 provides background information on Banks Peninsula, describes the selection of field sites, and provides further information on the specific study sites at Akaroa and on the Port Hills.
- 2) Chapter 3 examines the presence of seed limitation in populations of *C. vitalba*. Specifically, the effects of distance from the seed source, habitat type and site on the dispersal of *C. vitalba* seed were investigated by sampling natural seed dispersal. The presence of a short term and long term soil seed bank was also investigated.
- 3) Chapter 4 investigates the occurrence of microsite limitation in *C. vitalba*. This is accomplished by surveying the distribution of naturally occurring *C. vitalba* seedlings, measuring the growth of planted seedlings, and investigating the seedling emergence of *C. vitalba* using a manipulative experimental approach.
- 4) Chapter 5 discusses the implications associated with each of the above chapters and how they relate in the context of *C. vitalba* and in the wider field of invasion ecology.

## **CHAPTER TWO – Experimental Field Sites**

### **2.1 Banks Peninsula**

#### **2.1.1 Introduction to Banks Ecological Region**

Banks Peninsula is an area of dissected hill country of volcanic origin protruding into the Pacific Ocean from the eastern edge of the Canterbury Plains (Wilson, 2009). It is approximately 50 kilometres long and 30 kilometres wide (Wilson, 2009); an area of about 115,000 hectares. The bulk of the peninsula consists of eroded stumps of three Tertiary-age volcanoes which erupted onto much older sedimentary and volcanic surfaces between 15 and 6 million years ago (Wilson, 1999). The summits now crest between 500 – 900 metres above sea level (m.a.s.l.) with the highest point being Mount Herbert at 920 m (Wilson, 1999). The peninsula forms the distinctive Banks Ecological Region, which is divided into three ecological districts: Port Hills, Herbert and Akaroa (Wilson, 2009).

#### **2.1.2 Climate**

The climate varies across Banks peninsula, but some generalizations can be made. At sea level, the climate is temperate, subhumid and oceanic (Wilson, 1999). Rainfall increases from west to east - the Port Hills are much drier than the hills east of Akaroa - and average annual rainfall ranges from about 500 mm to 2000 mm. In winter, snow often lies for several days above about 500 m.a.s.l., but rarely falls at sea level (Wilson, 2009). Over most of the peninsula, winter ground frosts of minus several degrees Celsius are common. Recurrent droughts during summer are a feature of Canterbury's climate; the wettest parts of the peninsula are mostly protected against all but the harshest droughts (Wilson, 1999).

### **2.1.3 Soils**

The soil pattern across Banks Peninsula is complex, reflecting the variable topography, the thinning or removal of loess from steeper slopes, and sharp rainfall gradients (Wilson, 2009). Soils are derived from igneous bedrock and a mantle of loess: they are formed either on the volcanic rock itself, or on the mantle of loess which covers the rock in varying thicknesses up to several metres deep (Wilson, 1999). Soils are mostly of moderate to high fertility and are well-drained. The least fertile soils are those on rhyolite rock, and those occupying high, exposed slopes with a loess parent material, where natural fertility is reduced due to leaching. The most fertile soils occur on basalt rocks and on valley floors where thick recent alluvium has accumulated (Wilson, 1999).

### **2.1.4 Human impact on the landscape**

Prior to human habitation of Banks Peninsula, podocarp/hardwood forest covered most of the region, except in the southeast, where beech forest was quite extensive (Wilson, 2009). Polynesians arrived on Banks Peninsula about 1280 AD (Wilmshurst et al., 2008). During the following centuries of their occupation about one third of the virtually continuous forest cover across the Peninsula was cleared by fire (Wilson, 1999, 2009). No plant species are known to have become extinct during these times, but the fauna fared badly through habitat destruction and predation by the introduction of kiore (Polynesian rat) and kuri (Polynesian dog) (Wilson, 1999).

The earliest known European landing on Banks Peninsula was around 1815, and French and British colonists arrived about 1840 (Wilson, 1999). At this time, the peninsula was still predominantly forested, but between 1840 and 1900 nearly all the forest cover was destroyed and several plant species and more than a quarter of the native bird species on the peninsula disappeared (Wilson, 1999). Also during this time, many exotic flora and fauna species were introduced, such as *Mustela* spp. (stoat, weasel and ferret), *Ovis aries*

(sheep), *Felis catus* (domestic cat) *Poa* spp. (grass), and *Quercus* spp. (oak) among many others.

Milling of remnant old-growth forest continued well into the 1920s, and it is estimated that less than 1% of Banks Peninsula - about 1,100 hectares - remained under old-growth forest (Wilson, 2008). The forest cover became very fragmented, with remaining areas too small to support ecologically viable populations of native species (Pawson and Holland, 2008) and hundreds of exotic species naturalized and became part of the wild biota (Wilson, 1999). Since the 1980s, however, many areas on Banks Peninsula have revegetated and/or regenerated and now there is about 9,000 hectares of second-growth hardwood forests (Wilson, 2008).

### **2.1.5 Current vegetation types**

The peninsula landscape reflects about 700 years of human occupation: grazed pasture is currently the most extensive vegetation in the region (Wilson, 2009) (Table 2.1). Native tussocklands mostly occupy land that was deforested during Maori times but almost all the vegetation cover of the region now has a significant component of exotic species (Wilson, 2009). Nine thousand hectares are covered with second-growth hardwood forest, of which nearly 3,000 hectares are predominantly a *Kunzea ericoides* (kānuka) canopy and more than 6,000 hectares are under a mixed canopy of species such as *Melicytus ramiflorus* (mahoe), *Pseudopanax arboreus* (lowland fivefinger), *Hedycarya arborea* (pigeonwood), *Plagianthus regius* (ribbonwood), *Sophora* spp. (kowhai), *Pittosporum eugenioides* (lemonwood), *Ripogonum scandens* (also known as *Berchemia scandens*; supplejack), *Macropiper excelsum* (kawakawa) and *Cyathea dealbata* (silver tree fern) (Wilson, 2009) (plants names follow the Landcare Research New Zealand plant names database, see [www.landcareresearch.co.nz/databases/](http://www.landcareresearch.co.nz/databases/)). There is considerable regeneration of podocarps under these canopies, mostly of browse-resistant *Podocarpus totara* (lowland totara), and some *Prumnopitys taxifolia* (matai) (Wilson, 2009). Much of the second-growth bush is depleted of *Schefflera digitata* (sevenfinger), and *Dicksonia*

*squarrosa* (tree fern) by grazing farm stock, *Trichosurus vulpecula* (brushtail possum) and *Capra hircus* (feral goat) (Wilson, 2009). However, the regeneration of some native trees is favoured by moderate grazing and in many places *L. ericoides*, *H. populnea*, *P. totara* and *Pseudowintera* spp. (pepperwood) have established to form open treeland over grazed pasture (Wilson, 2009). Such treeland covers about 3,000 hectares of the peninsula.

Table 2.1 Proportions of the vegetation types in Banks Ecological Region, calculated from grid sampling in 1990 (Wilson, 2009).

<b>Vegetation Type</b>	<b>Total sites</b>	<b>%</b>	<b>Area (ha)</b>
Podocarp/hardwood forest	9	0.7	700
<i>Nothofagus</i> (beech) forest	1	0.1	100
Second-growth hardwood forest	115	9.1	9,100
- mixed	81	6.4	6,400
- <i>Kunzea ericoides</i> (kānuka) dominant	34	2.7	2,700
Treeland	34	2.7	2,700
Native scrub	35	2.7	2,700
Tussockland, grassland, fernland, shrubland	931	74.1	74,100
Wetlands	39	3.0	3,000
Exotic scrub	22	1.7	1,700
Exotic plantation	22	1.7	1,700
Discontinuous vegetation on rock, roads, farmland etc	53	4.2	4,200

At around 500 m.a.s.l. there is an abrupt transition from low-altitude forest to upper montane forest (Wilson, 2009). At this altitude, *P. totara* gives way to *P. hallii* (also known as *P. cunninghamii*; thin-bark totara), and *P. arboreus* to *P. colensoi* (mountain

fivefinger), and *M. ramiflorus* becomes sparse (Wilson, 2009). *Pseudowintera* spp. become very abundant, as do *Griselinia littoralis* (broadleaf), *Olearia ilicifolia* (mountain holly), *Polystichum* spp. (shield fern), *Blechnum discolor* (crown fern) and *Cyathea colensoi* (mountain tree fern) and *Cordyline indivisa* (mountain cabbage tree) (Wilson, 2009).

About 520 introduced vascular plant species have established as naturalised elements of the landscape, and of these, about 290 species are relatively widespread (Wilson, 2009). This total of about 520 naturalised plants is barely outnumbered by the 548 native species found on the peninsula (Wilson, 2009). Much of the open country is covered by Northern Hemisphere grasses (including *Lolium perenne*, *Dactylis glomerata* and *Poa* spp.), a scrubland of *Cytisus scoparius* (broom) and *Ulex europaeus* (gorse), *Berberis* spp. (barberry) and *Leycesteria formosa* (Himalayan honeysuckle). Timber plantations on the peninsula are mainly *Pinus* spp. (pines), and some Australian *Eucalyptus* spp. (eucalypt) and *Acacia melanoxylon* (blackwood) (Wilson, 1999). At least another 170 exotic species have established as casual garden escapees or as very local wild populations (Wilson, 2009).

Serious weed threats are widespread, such as *C. vitalba*, *Acer pseudoplatanus* (sycamore), *Berberis* spp. and *Cotoneaster* spp. (cotoneaster) (Wilson, 2009). Burning of weeds and scrubland causes a lot of damage and exotic forestry and wilding pine spread affect an increasing area of Banks Peninsula (Wilson, 2009). Ongoing damage to the native landscape is mainly caused by herbicide spraying and grazing in forest, scrub and wetland areas (Wilson, 2009).

## **2.2 Study sites and experiment conditions**

The number of accessible mature *C. vitalba* populations limited the number of sites available for study. In late 2008, the Christchurch City Council was contacted to find potential populations around Canterbury and study sites were confirmed at Akaroa and

the Port Hills over the summer of 2008/2009. The location of these sites on Banks Peninsula is shown in Fig. 2.1. The sites selected were based on the presence of *C. vitalba*, accessibility to the general public to the site, and access and permission granted by the Christchurch City Council.



Fig. 2.1 A satellite photograph of Banks Peninsula in Canterbury showing the location of the two study site locations – Port Hills and Akaroa - in relation to Christchurch.

Four sampling locations were divided between the two sites and two habitat types – open and forest (Table 2.2). The sites were all within a 250 m altitudinal range of each other. Only one location, L'Aube Hill Reserve at Akaroa, was accessible by the general public. Three locations, Sugarloaf Scenic Reserve (east gully), Reuter Reserve, and L'Aube Hill Reserve contained mature populations of *C. vitalba* and these sites were used for all

experiments. From hereon in, these locations will be referred to as follows: Sugarloaf Scenic Reserve east gully “Sugarloaf”, Reuter Reserve “Reuter Reserve”, and L’Aube Hill Reserve “Akaroa”.

A fourth location, Sugarloaf Scenic Reserve (west gully) “Sugarloaf west” was selected for the absence of *C. vitalba*. This location previously contained *C. vitalba*, but the Christchurch City Council and associated contractors destroyed all live *C. vitalba* plants in the late 1990s and early 2000s. This location has been clear of adult plants for more than eight years, with new seedling establishment regularly monitored and any young plants removed. This location was used only for measuring long distance seed dispersal into the site and the presence of a long-term soil seed bank.

Table 2.2 Summary of the two study areas used in this research, including site location, elevation in metres above sea level (m.a.s.l.) and the condition type for data collection.

Site	Location	Latitude and Longitude	Altitude (m.a.s.l.)	Experiment	Habitat
Akaroa	L’Aube Hill Reserve	43°48’11.14” S, 172°58’18.22” E	61	All	Open Forest
Port Hills	Sugarloaf Scenic Reserve (east gully)	43°36’27.71” S, 172°39’27.71” E	244	All	Open
Port Hills	Reuter Reserve	43°36’52.79” S 172°38’57.92” E	151	All	Forest
Port Hills	Sugarloaf Scenic Reserve (west gully)	43°36’19.68” S, 172°38’45.19” E	350	Seed dispersal and seed bank only	Forest



## **2.3 Akaroa Ecological District**

### **2.3.1 Introduction to Akaroa**

The Akaroa Ecological District is approximately 45,800 hectares of land which surrounds the water-filled basin of Akaroa Harbour, an eroded volcano crater (Wilson, 1992). About one-quarter of the land area slopes in toward the harbour basin and the remainder slopes outwards from the crater rim to open sea (Wilson, 1992). Average rainfall in the district is between 700 mm and 2000 mm: there is a steep rainfall gradient – annual rainfall can double over a distance of 3 km up an altitudinal range of 800 m (Wilson, 1992). There are numerous deep valleys, with reasonably extensive areas of alluvial flat land in their lower reaches (Wilson, 1992). The summits are often cloud-capped, and in winter snow may persist on the ground for weeks (Wilson, 1992). Some local sites are virtually frost-free, but other parts experience winter ground frosts down to -7°C (Wilson, 1992).

### **2.3.2 The landscape**

The original vegetation cover of Akaroa was mainly podocarp-hardwood forests, with some *Nothofagus* forests to the south west and east and lowland short tussock grassland to the south and west (McEwen, 1987). Permanently flowing streams descend all the main valleys, although streams in smaller valleys mostly dry up during the summer (Wilson, 2009). A lowland forest of *P. totara*, *P. taxifolia*, *Dacrycarpus dacrydioides* (kahikatea), *K. ericoides*, *M. ramiflorus*, *H. arborea*, and *G. littoralis* occupied the valley floors and most of the hilly slopes up to about 500 m (Leathwick et al., 2003; McEwen, 1987). Above this, montane podocarp/hardwood forest, dominated by *P. hallii* and with *Libocedrus* spp. (cedar) at the upper levels, was extensive (Leathwick et al., 2003; McEwen, 1987).

Formal settlement at Akaroa began with the arrival of the French in 1840 and the settlers found a landscape largely dominated by forest (Wilson, 2009). Accessible forests on the valley floors were cut first and mostly removed by 1880, followed by more inaccessible areas up until the 1920s (Wilson, 2009). Some cleared land reverted to regenerating scrub and forest, but repeated burning maintained areas of bracken fernland and tussock grassland (Wilson, 2008).

Current introduced weed species within the Akaroa region include *Fraxinus* spp. (ash), *Acer pseudoplatanus* (sycamore), *Rubus* spp, *Lonicera japonica* (Japanese honeysuckle), *Allium triquetrum* (onionweed), *C. vitalba*, *Tradescantia fluminensis* (wandering jew) and *Vinca major* (periwinkle).

### **2.3.3 L'Aube Hill Reserve**

L'Aube Hill Reserve is situated at the northern end of the Akaroa township (Fig. 2.3). The reserve is approximately 300 m x 400 m in size, is currently managed by the Christchurch City Council, and is surrounded by residential housing. The French Cemetery and associated walking tracks are located within the reserve and a shingle access road runs up the hill along the southern edge of the reserve. The dominant canopy species is *K. ericoides* with other canopy species such as *Myoporum laetum* (ngaio), *Quercus* spp., *Eucalyptus* spp (gum), some *Fraxinus* and *Pinus* spp. The understorey is composed mainly of *Coprosma rhamnoides* (red-fruited karamu), *C. robusta* (karamu), *C. lucida* (karamu), *Pittosporum tenuifolium* (black matipo), *P. arboreus* (five finger), *P. crassifolius* (lancewood) and *C. scoparius* and *U. europaeus*. Ground cover includes *Hedera helix* (ivy), *L. japonica*, *Passiflora mollissima* (banana passionfruit), *C. vitalba*, ferns, leaf litter, and in open areas exotic grasses.



Fig. 2.3 A satellite photograph of L'Aube Hill Reserve at Akaroa, Banks Peninsula, circled in red. The yellow rectangle marks the area used for data collection in this project.

## **2.4 Port Hills Ecological District**

### **2.4.1 Introduction to the Port Hills**

The Port Hills Ecological District has a total area of about 13,700 ha (Wilson, 1992). It is entirely hilly with slopes rising steeply from on the southern and eastern margins, and more gently on the northern and western margins (Wilson, 1992). The maximum altitude is 573 m.a.s.l. (McEwen, 1987) and the summits are often cloud-capped (Wilson, 1992). The climate is very dry with warm summers and cool winters with regular winter ground frosts and occasional light snowfalls (McEwen, 1987; Wilson, 1992). In most valleys, streams run through the winter but dry up over summer (Wilson, 1992). Annual rainfall

is approximately 600-1200 mm, and rainfall increases with increasing altitude from the north-eastern end of the district to the south-western end (Wilson, 1992).

The greater part of the Port Hills, like the rest of Banks Peninsula, were forested with podocarp/hardwood forest prior to human arrival (Wilson, 1992). This was mostly *P. totara*, *P. taxifolia*, *Dacrycarpus dacrydioides*, *M. ramiflorus*, *G. littoralis*, and *H. arborea*, with a montane forest composed of *P. hallii*, *G. littoralis*, and *Pseudowintera* spp. on the higher ground (Wilson, 1992). Polynesian settlers removed most of the forest from the northern slopes by burning after their arrival in 1280 AD (Wilmshurst et al., 2008; Wilson, 1992). European settlement at Lyttelton and then the establishment of Christchurch saw further modification of the vegetation. Continued burning resulted in the replacement of most forest with tussock grassland, however, some old-growth stands persisted (Knox and O'Connor, 2008). A fire in the late 1800s burned most of the remaining forest, and since that time, numerous smaller fires and more than a century of pastoral use have removed most of what remained of the original forest cover (Knox and O'Connor, 2008).

Much of the Port Hills district is now grazed, exotic forest planting has been extensive in the last few decades and urban settlement has spread along the north-facing slopes and along Lyttelton Harbour. Only small fragments of old-growth forest remain (Wilson, 1992). Most of the original *Poa cita* (silver tussock) tussockland has been thinned out with intertussock pasture (Wilson, 1992). In the last few decades, a patchwork of small bush reserves managed by the Christchurch City Council, the Department of Conservation and private trusts have been substantially augmented by several major conservation initiatives (Knox and O'Connor, 2008). The Summit Road Society, for example, has purchased several hundred hectares of regenerating forest and has completed a vigorous replanting programme (Knox and O'Connor, 2008).

#### 2.4.2 Sugarloaf Scenic Reserve and Reuter Reserve

Sugarloaf Scenic Reserve (“Sugarloaf”) and Reuter Reserve are located on south-facing slopes of the Port Hills and are both managed by the Christchurch City Council (Fig 2.5 and 2.6). The only public walking tracks in Sugarloaf are the Crater Rim Walkway and Mitchells Track, which are both located in the upper part of the reserve. There are no public walking tracks located in Reuter Reserve, however, above and below Reuter Reserve is residential housing and small pockets of farmland, and the access road leading down into the reserve is privately owned. Reuter Reserve is approximately 3 ha and Sugarloaf is approximately 111 ha, with fairly extensive areas of mostly second-growth mixed hardwood forest, native scrub with abundant *Hebe strictissima*, small pockets of *K. ericoides*, some large stands of *Phormium tenax* (New Zealand flax), and much pasture (Wilson, 1992). A *M. ramiflorus* mixed broadleaf forest centered on the main gully with extensive areas of unimproved pasture dominated by *Dactylis glomerata* (cocksfoot grass), with *P. cita*, *Discaria toumatou* (matagouri) and *P. tenax* also present on the surrounding slopes (Reay and Norton, 1999). There are many introduced weed species in the reserves, including *Rubus* spp., *C. scoparius* and *U. europaeus*, *Chrysanthemoides monilifera* (boneseed), *C. vitalba*, *Berberis* spp., *Pinus radiata*, *Sambucus nigra* (elderberry), *Ribes sanguineum* (flowering currant), and *Celastrus orbiculatus* (spindleberry) (Wilson, 1992).

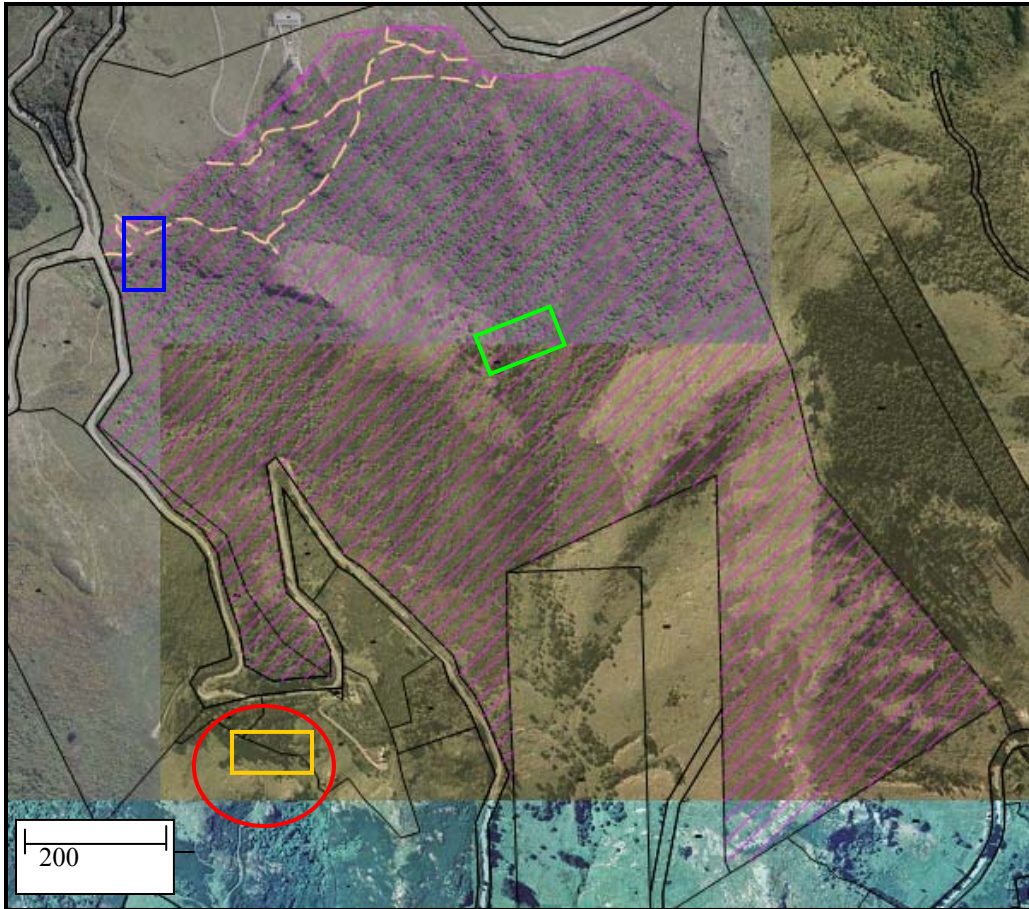


Figure 2.5 Sugarloaf Scenic Reserve (shaded pink) and Reuter Reserve (red circle) on the Port Hills, Christchurch. The yellow dotted line marks public walking tracks through the upper part of Sugarloaf. Dyers Pass Road runs along the left side of Sugarloaf and separates Sugarloaf and Reuter Reserve. Data collection points at Sugarloaf are marked by the green (east gully) and blue (west gully) rectangles. The data collection point at Reuter Reserve is marked by the yellow rectangle.

## CHAPTER 3 – Seed limitation in *Clematis vitalba*

### 3.1 INTRODUCTION

As outlined in Chapter 1, the successful invasion of environmental weeds has been correlated with traits such as prolific seed production and dispersal (McAlpine and Jesson, 2008). Weed species are frequently well-adapted for the efficient dispersal of their seed by multiple vectors, which can result in widespread seed-deposition, and thus enhance the chances of invasion success (McAlpine and Jesson, 2008). Producing high quantities of seed assists the maintenance of high plant densities, while seed dormancy and seed banks are important in seedling recruitment (Martínez-Ghersa and Ghersa, 2006).

The initial stage of seedling recruitment – after seed production – is seed dispersal, which is generally considered an adaptation to increase the probability of offspring survival (McAlpine and Jesson, 2008). Seed dispersal determines the potential rates of recruitment, invasion, range expansion and gene flow in plant populations (Levey et al., 2008). The spread to variable environments in large numbers increases the chances of successful invasion (Martínez-Ghersa and Ghersa, 2006). *Clematis vitalba* is a prolific seeder and the dispersal of seeds by wind is a significant means of allowing plants to establish over a wide area (Stein, 2004).

After mature seeds are dispersed from the parent plant, germination may occur immediately or be delayed for an indefinite period (Fenner and Thompson, 2005). During this period of delayed germination, ungerminated seeds on or in the soil are said to form a soil seed bank (Baker, 1989; Fenner and Thompson, 2005). Seed banks are classified into three broad groups: transient, short-term persistent, and long-term persistent (McAlpine and Jesson, 2008). Seeds which form transient seed banks do not persist in the soil for more than a year (Baskin and Baskin, 1998). Seeds in short-term persistent seed banks survive in the soil for at least one year but less than five years, while a long-term persistent

seed bank consists of seeds which can survive for at least five years (Baskin and Baskin, 1998).

A combined strategy of high reproductive potential and seed dormancy allows the presence of a large and relatively constant seed bank (Martínez-Ghersa and Ghersa, 2006) and studies of natural seed banks can provide direct evidence of seed longevity in the soil (Fenner and Thompson, 2005). Seed dormancy occurs when a precise set of germination conditions are not met. Seed dormancy is displayed by *C. vitalba* and can be reduced by a range of factors, of which chilling, light and nitrate are the three most widely reported (Bungard et al., 1997a). A chilling requirement for germination has obvious potential ecological benefits for species growing in seasonal climates, where germination does not occur until after winter when temperatures and light levels are more suitable for seedling growth and survival.

The seed of *C. vitalba* has a high degree of seed dormancy, which is a common characteristic of many successful weed species (Bungard et al., 1997a). Germination of the seed is stimulated by moist chilling at 1-5°C for two to five months (Bungard et al., 1997a). The presence of a persistent seed bank for this species has been debated in the literature to date. Bungard et al. (1997a) claims that seeds retained on the vine over winter act as an aerial or canopy seed bank; this trait is present in about 1200 species worldwide (Lamont and Enright, 2000). However, Stein (2004) claims that dispersed seed form a seed bank which can lie dormant for a number of years. West (1992) found approximately eight times more seed in the soil than that which was dispersed in the study year and suggested that *C. vitalba* seed can survive for at least five years in soil. The life of a seed bank has important implications for the management of invasive species, because eradication programmes have to continue for at least as long as the life of the seed bank if they are to succeed (McAlpine and Jesson, 2008).



### 3.1.1 Objectives

This chapter explores the degree of seed limitation in *C. vitalba* and investigates how both spatial and temporal seed dispersal influence the population abundance and range spread of this species. Specific questions are:

- (1) How does variation in distance from the seed source affect the seed dispersal of *C. vitalba*?
- (2) Does habitat type have an effect on seed dispersal? Which habitat type allows for the most efficient seed dispersal?
- (3) Are *C. vitalba* seeds present in the soil one year after seed dispersal? If so, does *C. vitalba* have a short-term or long-term soil seed bank?

## 3.2 EXPERIMENT DESIGN AND LAYOUT

In each habitat at each site, three flowering *C. vitalba* vines were selected for data collection (see Chapter 2 for site and habitat information). Selection criteria for a *C. vitalba* vine ('focal plant') included: it must be in flower; it must be 30 m or further from the nearest other flowering *C. vitalba* vine; and the earth at the base of the focal plant must be workable soil.

A 30 m transect was marked out in an approximate straight line away from each focal plant and four sampling positions were marked every 10 m along the transect (Fig. 3.1). At Port Hills east, where all adult plants were killed some years ago, the remnants of three dead *C. vitalba* vines were selected under the following criteria: it must be at least 30 m from the nearest other dead *C. vitalba* vine, and the earth at the base of the focal plant must be workable soil. A 30 m transect was marked out in an approximate straight line away from

each replication, and four sampling positions were marked out as described above. These focal plants were used to collect data for the following two seed limitation experiments.

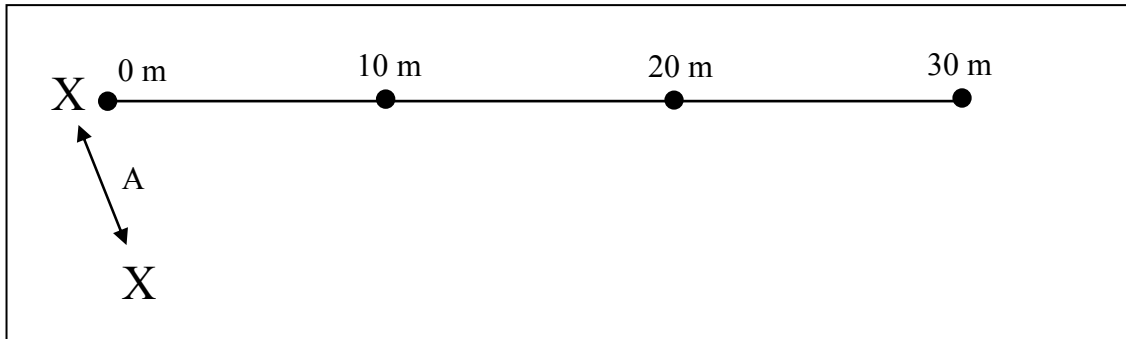


Fig. 3.1 The layout of a 30 m transect for sampling of the soil seed bank and measuring seed dispersal at four sites on Banks Peninsula in 2009. X = *Clematis vitalba* focal plant. A = a distance of at least 30 m between focal plants and/or other flowering *C. vitalba* vines.

### 3.2.1 Sampling the soil seed bank

The presence of a soil seed bank was determined by removing soil samples at all the sampling points described above. *Clematis vitalba* on Banks Peninsula typically flowers over summer between January and March and flowers were observed on the vines as late as 4 May 2009. Soil samples were taken at each site while *C. vitalba* vines were still in flower and/or just as seed began to set (26 March at Sugarloaf, 29 March at Port Hills west, 31 March at Reuter Reserve and 6 April at Akaroa). This was to ensure no contamination of the soil from that year's seed; the aim of this experiment was to determine the presence of a soil seed bank of at least one year. Samples were taken using a soil corer with a diameter of 7.5 cm. At each sampling point, four soil samples were taken randomly within a 1 m x 1 m area. The leaf litter layer was removed before sampling and the soil corer was driven into the soil to a depth of 8 cm. The soil collected at all sites was dry and loose.

These four samples were combined into one larger sample for each sampling point. The samples were stored in airtight plastic bags at room temperature for up to two weeks.

The size of the soil seed bank was estimated by a seedling germination method. Soil samples were sieved through a coarse sieve (4mm mesh width) to remove bulky soil and plant material. At the time of sieving, all soils were relatively equally dry, loose and crumbly. The weight of the dry sieved sample was recorded and each sample was spread into a layer of approximately 5 mm thickness on a tray filled with unfertilized potting soil. A fine layer of gravel was laid over each soil sample to limit the growth of *Marchantia* species. All soil samples were set out in separate trays using this method. The trays were placed in a heated glasshouse with a daytime temperature of 20-22°C and a night time temperature of 10-15°C on 6 and 7 April 2009 and were watered daily. Seedling germination was monitored on a weekly basis. Once they were large enough to identify, all seedlings that germinated were carefully removed from each tray to avoid disturbance and or/removal of other seeds in the soil. The germination of all *C. vitalba* seedlings was recorded.

Little germination had occurred after 12 weeks so the samples were chilled outdoors from 7 July to 30 September 2009. Bungard et al. (1997b) found that the chilling of *C. vitalba* seed for 12 weeks at 5°C increased germination of the seed from 3% to 64%. Trays were placed outdoors and covered with wire mesh to minimize disturbance of the samples by plant debris and animals. During this time the maximum daytime temperature was approximately 14°C and the minimum night-time temperature was approximately -3 °C. Precipitation for the month of July was approximately 68 mm, for August 60 mm and September 42 mm. The average monthly percentage of sunshine was 43-45%. The trays were checked on a weekly basis and any debris which collected on top of the wire mesh was removed. No germination of *C. vitalba* occurred over this chilling period, however, the germination of a variety of other species occurred. All seedlings were carefully removed when large enough to identify.

The trays were returned to the heated glasshouse on 30 September 2009. Seedling germination was monitored on a weekly basis, and again, as seedlings became large enough to identify, they were removed and *C. vitalba* seedlings were recorded. To bring seeds that may have been buried deeper in the samples to the surface, all samples were stirred on 2 December 2009 and again on 30 December 2009. After each sample was stirred, the soil was carefully spread out again in an even layer. A final count of *C. vitalba* seedlings was taken on 13 January 2010, and the soil samples were disposed of.

### **3.2.2 Collecting dispersed seeds**

Seed dispersal was measured using sticky seed traps set out at the sampling points described above. Seed traps are widely used in dispersal studies as they provide a reliable estimate of the diaspore rain at a given location (Lemke et al., 2009). A common type of seed trap is the sticky trap, where a surface is coated with an adhesive and placed on or near the soil surface (Huenneke and Graham, 1987). Sticky traps perform well in capturing small, lightweight seeds, particularly those with awns or ornamentation (Huenneke and Graham, 1987), as is typical of *C. vitalba*. For this experiment, a sticky trap was constructed out of plastic trellis, OHP transparency paper approximately 29.7 cm x 21.0 cm and garden wire. The trellis base of each trap was 35 cm by 25 cm and a sheet OHP transparency was secured to the trellis base using garden wire. At each sampling position, a sticky trap was secured to the ground with four metal pegs approximately 10cm in length and Tanglefoot Tangle Trap Insect Trap Coating ('Tangle Trap') was applied evenly with a paintbrush to the entire upward-facing surface of the OHP transparency. Tangle Trap is an organic, clear, odourless substance designed to trap insects and can endure all weather and temperature changes. All traps at all sites were set out as above. Trap set-up was completed on 26 March 2009 at Sugarloaf, 29 March at Port Hills west, 31 March at Reuter Reserve and 6 April at Akaroa.

The sticky traps were exchanged for a new trap set out in the same position using the same method as described above. The exchange occurred approximately 13 weeks after the initial set-up, on 29 June at Port Hills open, 3 July at Port Hills west and 5 July at Akaroa open and forest. When each trap was removed from its position, it was tagged with its location details and wrapped securely in plastic film wrap to prevent the loss of any seeds from the trap. The traps were taken to the lab and all material on each trap was examined and intact *C. vitalba* seeds were counted. The second round of sticky traps were removed approximately 10 weeks after they were set-out in the field, on 14 September at Port Hills forest, 15 September at Port Hills open, 17 September at Port Hills west and 19 September at Akaroa open and forest. Again, each trap was taken to the lab and *C. vitalba* seeds were counted. Totals for the two dates were combined into one number per sampling point for analysis.

### **3.2.3 Statistical analyses**

Statistical analyses were performed in the statistical package R version 2.9.1. Generalised Linear Models (GLMs) were used to estimate the number of seedlings per kilogram of soil and the influence of distance from the seed source on the soil seed bank. This was compared between habitat types and sites. GLMs were also used to examine the influence of distance and habitat type on the dispersal of seeds away from a parent vine. A quasipoisson error distribution was fitted when needed to allow for the over-dispersion of the data. The fit of all models was tested using Chi-square tests.

### 3.3 RESULTS

#### 3.3.1 Short term soil seed bank

Three seeds germinated in the samples taken from Akaroa during the first 12 weeks of this trial. No germination occurred between 7 July and 30 September when the samples were chilled outdoors. The majority of seed germination occurred during November, approximately six weeks after the samples had been returned to the heated glasshouse, and some germination occurred in December. Seventeen out of 60 soil samples contained viable *C. vitalba* seed. A total of 77 *C. vitalba* seeds germinated from 60 samples over the course of 36 weeks; 72 of these occurred in samples taken from Akaroa and the remaining 5 germinated from Reuter Reserve samples. Nearly three-quarters of the samples that contained *C. vitalba* seed were samples taken from the forest habitat. No seeds germinated in the 12 samples taken from Sugarloaf.

Soil samples taken from Akaroa contained significantly more seeds than those taken from the Port Hills (Fig 3.1). Soil samples from the forest habitat at both Akaroa and Reuter Reserve contained significantly more seeds than those taken from the open habitat.

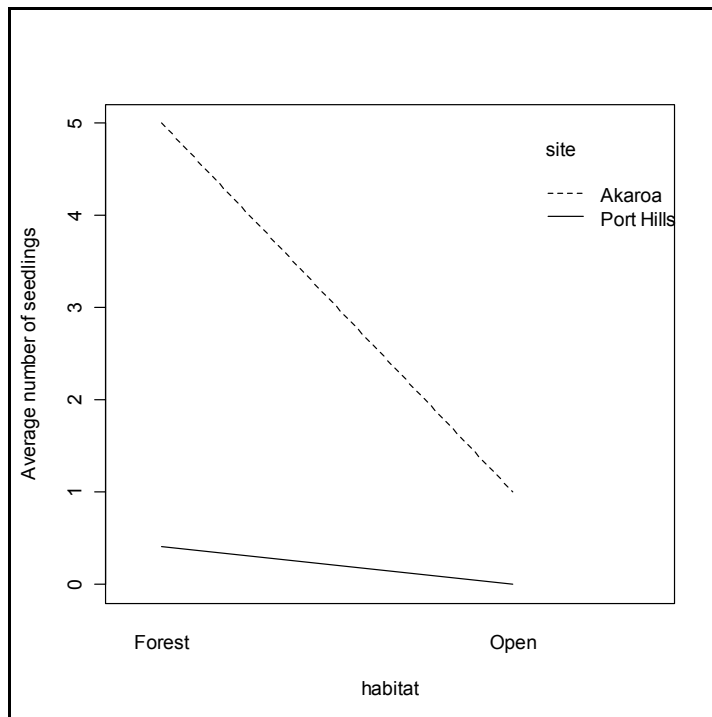


Fig. 3.1 The average number of seedlings per kilogram of soil in two habitat types at two sites on Banks Peninsula in 2009. Soil samples were taken from within the forest and open habitats at L'Aube Hill Reserve, Akaroa, from the forest habitat at Reuter Reserve, Port Hills and from the open habitat at Sugarloaf Scenic Reserve, Port Hills.

The density of seeds per kilogram of soil in the soil seed bank varied between site and habitat type (Table 3.1). Only two out of three predictors had a significant effect on the density of seeds present in the soil; site and habitat. Distance was not significant, and the interactions between these three predictors were also not significant.

Table 3.1 Variation in the density of *Clematis vitalba* seed per kilogram of soil estimated from soil samples taken in 2009 at two sites on Banks Peninsula, from a quasipoisson Generalized Linear Model.

A: Analysis of Deviance Table

	DF	Deviance	Residual DF	Residual Deviance	P(> Chi )
NULL			47	363.80	
Site	1	112.65	46	251.15	<0.001
Habitat	1	66.61	45	184.54	<0.001
Distance	1	3.33	44	181.22	0.36
Site * habitat	1	2.67	43	178.54	0.41
Site * distance	1	3.05	42	175.50	0.38
Habitat * distance	1	0.60	41	174.90	0.70
Site * habitat * distance	1	<0.001	40	174.90	1.00

B: Coefficients Table

	Estimate	Standard Error	t value	Pr(> t )
(Intercept)	3.864e-01	7.894e-01	0.489	0.6272
Site - Sugarloaf	-1.769e+01	3.346e+03	-0.005	0.9958
Habitat - forest	1.903e+00	8.503e-01	2.238	0.0309
Distance	3.481e-03	4.143e-02	0.084	0.9334
Site - Sugarloaf * habitat - forest	1.579e+01	3.346e+03	0.005	0.9963
Site - Sugarloaf * distance	-3.481e-03	1.789e+02	-1.95e-05	1.0000
Habitat - forest * distance	-1.753e-02	4.528e-02	0.387	0.7008
Site - Sugarloaf * habitat - forest * distance	-5.836e-02	1.789e+02	-3.26e-04	0.9997



### 3.3.2 Long term soil seed bank

Twelve soil samples were also taken Port Hills west where mature *C. vitalba* plants had been absent for eight years at the date of sampling. The samples were taken from the forest habitat within an area of approximately 2275 m<sup>2</sup> in size. A total of 7565 grams of soil was taken from the site, with individual soil samples weighing between 490 and 825 grams. These twelve samples did not contain *C. vitalba* seed that germinated during the 36-week trial, and therefore, no analysis was completed on this data set.

As a comparison, of the other 24 samples taken on the Port Hills, only four of them contained *C. vitalba* seed and all these four samples were taken from within the forest habitat. A Fisher exact test gave a P value of 0.0466; the sample size at this site was sufficient to detect a seed bank. Significantly less germination occurred here than at Sugarloaf and Reuter Reserve.

### 3.3.3 Seed dispersal

The dispersal of seed was measured for 23 weeks during seed fall between April and September in 2009. During that time, a total of 2455 *C. vitalba* seeds were caught. Of this total, 2007 seeds (82 per cent) were caught at Akaroa, and 75 per cent of seeds across all sites were caught in the forest habitat. There were five seed traps that did not catch any *C. vitalba* seed; two at the Port Hills forest site, one at Akaroa open and two at Akaroa forest.

The number of seeds caught varied significantly between sites, habitat types and distance from the seed source (Table 3.4). Akaroa caught significantly more *C. vitalba* seeds than the Port Hills and the traps in the forest habitat caught significantly more seed than those in the open habitat (Fig. 3.2). There was a gradual decrease in seeds caught as distance from the seed source increases (Fig. 3.3). The interactions between site, habitat, and distance were not significant.

Table 3.4 Variation in *Clematis vitalba* seeds caught in sticky seed traps from 26 March to 19 September 2009 at two in two habitat types at sites on Banks Peninsula, from a quasipoisson General Linear Model.

A: Analysis of Deviance Table

	DF	Deviance	Residual DF	Residual Deviance	P(> Chi )
NULL			47	4976.1	
Site	1	1070.4	46	3905.7	<0.001
Habitat	1	682.0	45	3223.7	<0.001
Distance	1	389.6	44	2834.1	<0.001
Site * habitat	1	134.3	43	2699.9	0.2
Site * distance	1	66.9	42	2632.9	0.3
Habitat * distance	1	3.0	41	2629.9	0.8
Site * habitat * distance	1	133.9	40	2496.0	0.2

B: Coefficients Table

	Estimate	Standard Error	t value	Pr(> t )
(Intercept)	5.33415	0.29715	17.951	<0.001
Site - Port Hills	-1.93963	0.83552	-2.321	0.0254
Habitat - open	-1.64028	0.71957	-2.280	0.0280
Distance	-0.03308	0.01939	-1.706	0.0957
Site - Port Hills * habitat - open	2.29207	1.23354	1.858	0.0705
Site - Port Hills * distance	0.00233	0.05379	0.043	0.9657
Habitat - open * distance	0.01737	0.04293	0.405	0.6880
Site - Port Hills * habitat - open * distance	-0.15809	0.13274	-1.191	0.2407

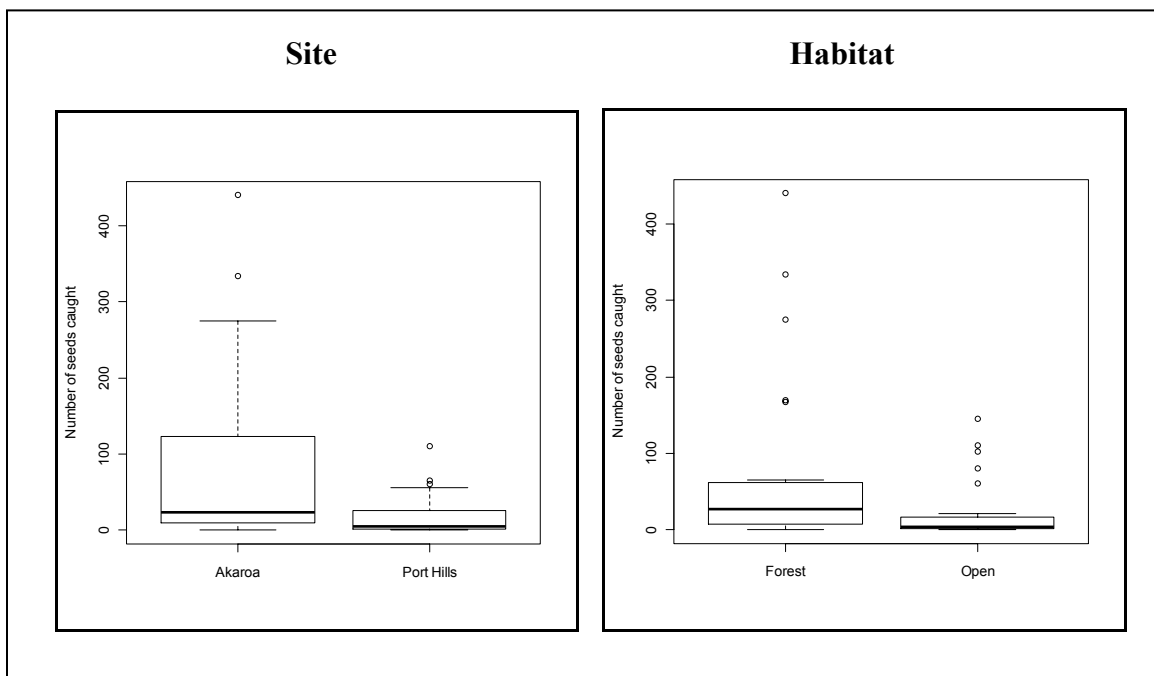


Fig 3.2. A box and whisker plot showing variation in the seed catch per trap of *Clematis vitalba* between 26 March and 19 September 2009 at two Banks Peninsula sites. The middle horizontal line within the box shows the median seed catch rate. Also shown are the upper and lower quartiles (lines either side of the median), and whiskers encompassing 95% range of the data (designated by dashed lines), with outliers that fall beyond the 95% range indicated by the open dots. Both main effects were significant, see table 3.4A.

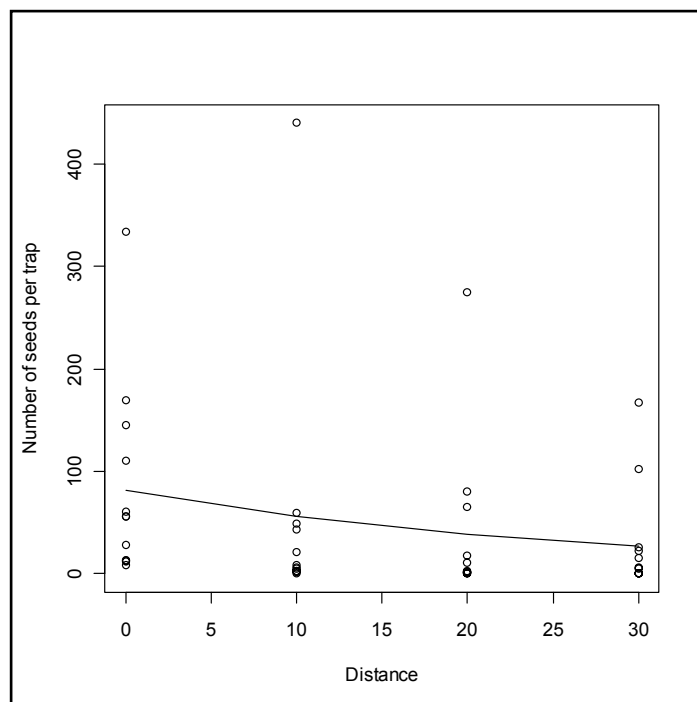


Fig. 3.3 Counts of *Clematis vitalba* seed caught in sticky seed traps (each 623.7 cm<sup>2</sup> in size) at two Banks Peninsula sites during April - September 2009. The line of best fit, from a quasipoisson Generalized Linear Model given in Table 3.4, shows a significant gradual decrease in seeds caught as distance from the seed source increases.

Sticky seed traps were also set up in the forest habitat at Port Hills west, about 500 m from the nearest flowering adult plants. Seven *C. vitalba* seeds were caught in three traps which gives an average of 0.58 for this site. This can be compared to an average of 135 *C. vitalba* seeds in the forest at Akaroa, and an average of 19.92 *C. vitalba* seeds in the forest at Reuter Reserve. The seeds caught at Port Hills west were significantly more than expected from local dispersal (Fig. 3.5).

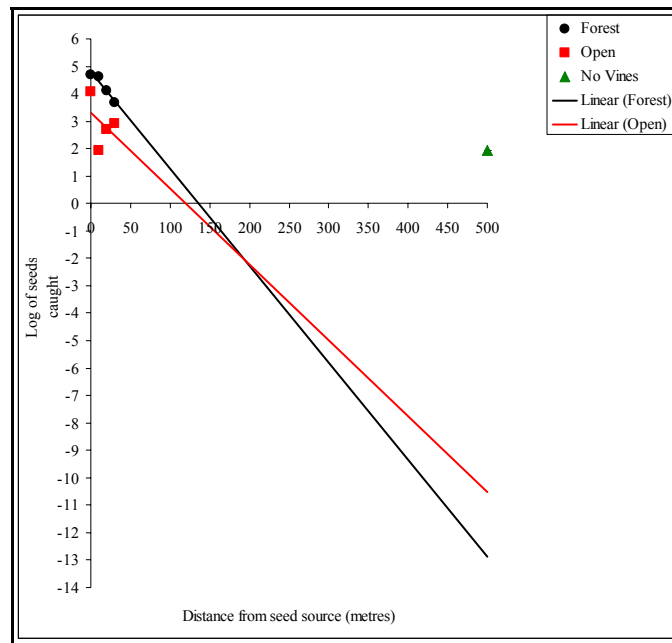


Fig 3.5 The effect of distance on seed dispersal of *Clematis vitalba* at two sites on Banks Peninsula between April and September 2009. Remote seed dispersal occurs at Sugarloaf Scenic Reserve (west gully) from a seed source approximately 500 m away.

### 3.4 DISCUSSION

#### 3.4.1 Seed dispersal

A large number of seeds were trapped at two sites on Banks Peninsula with mature stands of *C. vitalba*. This study found an average of 2998 seeds per m<sup>2</sup> caught directly under the seed source in the forest and an average of 914 seeds per m<sup>2</sup> in the open at Akaroa. An average of 1010 seeds per m<sup>2</sup> were found directly under the seed source in the forest on the Port Hills and 497 seeds per m<sup>2</sup> in the open on the Port Hills. This supports previous claims that *C. vitalba* is a prolific seed producer with very effective dispersal mechanisms. This study found a larger number of *C. vitalba* seeds were dispersed, with an average of

1242 seeds trapped per m<sup>2</sup> in the forest and 398 seeds per m<sup>2</sup> in the open across all distances on Banks Peninsula. This can be compared to a study by West (1992), where an average of 65 seeds per m<sup>2</sup> were found in seed traps in the forest in the Rai Valley in Marlborough.

Dispersal of *C. vitalba* seeds away from the seed source was evident in this study; widespread dispersal is a key trait in the invasiveness of this species. At Port Hills west, where no live *C. vitalba* vines were present, *C. vitalba* seed was still trapped, which indicates that this species achieves effective long-distance dispersal. A high number of seeds were dispersed up to 30 m from the seed source, and seeds were also detected up to approximately 500 m away. Seed density almost always declines with distance, with an extended tail of long-distance dispersal (Nathan and Muller-Landau, 2000). A distance effect is evident in this species and seed dispersal was found to occur at distances that were not expected. Similarly, McAlpine and Jesson (2008) found that the dispersal curve for *B. darwinii* was more drawn out than expected; many seeds were dispersed up to 150 m from the parent plant but *B. darwinii* seeds were consistently detected at a distance of 450 m.

Long-distance dispersal (LDD) or fat tail dispersal – dispersal beyond the local patch or cluster of conspecifics – is disproportionately important for several ecological processes, including range expansion (Muller-Landau et al., 2003). Long distance dispersal can accelerate the invasion process by initiating new “satellite” populations and is thought to be disproportionately important to a range of recruitment processes (Clark et al., 1998). Information in relation to fat tail or long-distance dispersal (LDD) is crucial to understanding aspects of the biology of plants, such as the dynamics of metapopulations and the spread of invasive species (Cain et al., 2000). Research into LDD is severely constrained by data limitations. Estimating the trend of dispersal is important yet challenging; estimating deviations from the trend is even more important and challenging (Nathan, 2006).

### 3.4.2 Soil seed bank

Soil samples taken from the Port Hills and Akaroa sites contained low amounts of *C. vitalba* seed, providing evidence that this species has a small short-term soil seed bank. This is an important discovery as there is some confusion in the literature regarding the presence of a soil seed bank (see Bungard et al., 1997a; Stein, 2004; and West, 1992). The soil taken from Port Hills west was found to be absent of *C. vitalba*, which would indicate that *C. vitalba* seed cannot survive for eight years in the soil. The occurrence of a small short soil seed bank could be one reason for the discrepancy in the literature; it is possible that previous studies did not encounter a soil seed bank as the number of seeds retained in the soil is low.

The soil seed bank can be compared to the average dispersal of seed per m<sup>2</sup>. An average of 2998 seeds per m<sup>2</sup> were caught directly under the seed source in the forest and an average of 914 seeds per m<sup>2</sup> in the open at Akaroa, while, under the seed source, an average of 0.02 seedlings per m<sup>2</sup> were found in the forest and an average of 0.005 seedlings per m<sup>2</sup> were found in the open at Akaroa. A smaller number of seeds were both trapped and found in the soil seed bank on the Port Hills. An average of 1010 seeds per m<sup>2</sup> were found directly under the seed source in the forest and 497 seeds per m<sup>2</sup> in the open, while an average of 0.005 seedlings per m<sup>2</sup> were found in the forest and 0.0 seedlings were found in the open. West (1992) found eight times more seed in the seed bank than fell in the year of her study. My data are more consistent with the seed bank being small and short-term, so the seed bank does not increase with several years' input.

There are several reasons for the varying results found between studies. It is interesting that West (1992) found a significant soil seed bank of approximately eight times that of seed fall, while this study found a very small seed bank. The study by West (1992) was carried out in Marlborough, temporal variation in dispersion patterns of seed dispersal and the soil seed bank may have contributed to the observed differences in trapped seeds. Such variation can arise from differences in the relative seed output of individuals over time or

from differences in the seed-dispersal process itself (Nathan and Muller-Landau, 2000). Also, seed output varies considerably among plants. Variation within populations is determined partly by plant size; site quality influences plant size and also has a direct effect on resources available for reproduction, for example, light availability or nutrients (Nathan and Muller-Landau, 2000). In any case, my results are more consistent with those of West (1992) who also found a soil seed bank than with Bungard et al (1997a) who reported no soil seed bank for this species.



## **CHAPTER 4 – To what extent is *Clematis vitalba* microsite limited?**

### **4.1 INTRODUCTION**

As outlined in Chapter 1, population size at a local scale is constrained in part by the availability of opportunities for establishment and growth (Münzbergová and Herben, 2005). The events that determine the different fates of individual plants frequently occur during the period of the life cycle encompassing seed dispersal, germination and seedling establishment (Harper, 1977). The availability of suitable microsites on a soil surface regulates the number of plants establishing from seed (Harper et al., 1965a). Thus, the nature of the environment immediately surrounding a seed or seedling are of critical importance in determining the dynamics of plant populations (Fowler, 1988).

#### **4.1.1 Safe sites for germination**

At the scale of the size of a seed, soil environments are highly heterogeneous and the environment immediately surrounding a seed determines whether it receives the conditions, resources and stimuli needed for germination (Harper, 1977). This heterogeneity in the micro-environment, combined with germination requirements can itself determine the proportion of seeds which germinate immediately after dispersal and those which form the soil seed bank. Changes in the physical environment, for example, an increase in temperature or exposure, change the frequency of safe sites in the soil environment and so alter the probabilities of a seed forming an established seedling (Harper, 1977).

Seed germination and plant establishment usually depend on the environmental conditions in the immediate vicinity of the seed (Jones and del Moral, 2005). Due to small-scale

environmental heterogeneity, some microsites are more favourable to seed germination or seedling establishment than others (Harper et al., 1965a). The availability of suitable microsites on a soil surface regulates establishment (Harper et al., 1965a). Physical features such as amount of litter, presence of debris and soil texture are important characteristics of microsites that can affect seedling establishment (Jones and del Moral, 2005). The presence of other vegetation can also create variation in microclimatic conditions and strongly influence seed recruitment, germination and establishment (Jones and del Moral, 2005). Other vegetation can ameliorate environmental extremes, facilitating germination by acting as a 'nurse plant' by shading or adding nutrients to the soil (Niering et al., 1963), however, other vegetation can also compete for resources with new seedlings. Existing vegetation can also create safe sites by trapping seeds; this can lead to increased germination in these sites by simply increasing the number of seeds present (Jones and del Moral, 2005).

The individual seed germinates in response to the precise set of conditions it experiences in its immediate environment (Naylor, 1985). Probably the most crucial factor in determining the germination of seeds in the soil is a suitable combination of temperature and moisture (Mayer and Poljakoff-Mayber, 1989). Among the conditions required for germination are: an adequate supply of water, a suitable temperature, and for some seeds, light (Mayer and Poljakoff-Mayber, 1989). The seed of *C. vitalba*, which displays embryo-dormancy, requires moist chilling at 1-5°C for between 2-5 months in order to stimulate germination (Bungard et al., 1997b). According to Bungard et al. (1997b), the high level of dormancy in *C. vitalba* seeds, and the limited ability of light and nitrate to overcome this dormancy in the absence of chilling, suggest that dormancy is an effective mechanism reducing germination prior to winter, and subsequently, seedling mortality due to unfavourable conditions.

#### **4.1.2 Seedling establishment and survival**

Seedling establishment can be affected by many abiotic and biotic factors, such as leaf litter, light, microclimate, soil characteristics, and pathogens (Gómez-Aparicio et al., 2005). For example, a study by McAlpine and Jesson (2008) found that microsite availability can limit invasion success in bird-dispersed species, and successful recruitment of *Berberis darwinii* (Darwin's barberry) depended on the dispersal of seeds away from the parent canopy to areas of high light. An examination of which microsites constitute suitable sites for seedling establishment is essential to understand the structure and dynamics of plant populations (Gómez-Aparicio et al., 2005).

The establishment of a seedling from a seed involved a series of precise deterministic events within an environment in which the scale of heterogeneity is determined by the size of the seed (Harper, 1977). The presence or absence and the density of a seedling population depends not only on the availability of seed but on the frequency of safe sites that provide the precise conditions required by a particular seed. From among the vast numbers of seed present in the soil and arriving on the surface through dispersal, only a tiny fraction germinates to give seedlings (Harper, 1977). The development of seedling from a seed depends on conditions which are immediately localized to the environment of that seed and seedling.

#### **4.1.3 Objectives**

In general, this chapter investigates the degree of microsite limitation in the population abundance and spread of *C. vitalba* on Banks Peninsula. This chapter aims to explore the impacts of the type of habitat (forest, edge and open) on the rate of seedling emergence from added seed, on the distribution of naturally occurring seedlings, and on the survival and growth of transplanted seedlings. More specifically, the aims of this chapter were:

- 1) To determine how site, habitat type and distance from the seed source affects the density and distribution of naturally occurring *C. vitalba* seedlings.
- 2) To investigate the survival rate and growth of transplanted *C. vitalba* seedlings in three habitat types.
- 3) To explore the effect of habitat type and site on the seedling emergence of *C. vitalba* seeds.

## **4.2 EXPERIMENT DESIGN AND LAYOUT**

### **4.2.1 Seedling distribution surveys**

Seedling distribution surveys were completed at Akaroa on 4 May 2009 and the Port Hills on 7 May 2009. Mature seed sources were randomly selected within the two habitat types – open and forest – at each site. At Sugarloaf and Reuter Reserve 12 transects were completed, six in each habitat type, and 11 transects were completed at Akaroa, six in the forest habitat and five in the open habitat. A 30 m transect was set out in an approximate straight line from each seed source. Plots of 1 m x 1 m were laid out along the transect starting from the seed source and *C. vitalba* seedlings under 1 m in stem length were recorded within each plot.

### **4.2.2 Seedling survival and growth**

Approximately 200 *C. vitalba* seeds were collected at L'Aube Hill Reserve, Akaroa in July 2008. They were stored dry at room temperature in a sealed plastic bag for approximately one month before use. On 8 August 2008, the seeds were planted in multi-celled plastic

trays filled with a fertilized potting soil. One seed with the seed tail removed was planted in each cell at a depth of approximately 5 mm. The trays were placed in a heated glasshouse with a daytime temperature of 20-22°C and a night-time temperature of 10-15°C and were watered daily.

On 7 May 2009, 81 *C. vitalba* seedlings were planted into L'Aube Hill Reserve, Akaroa. As 90 *C. vitalba* seedlings were available for this experiment, only the site at Akaroa was used. Three 1 m x 1 m plots were marked out in each of the three habitat types (Fig. 4.1). The forest and open plots were marked out at least 3 m from the forest edge in their respective habitats (see A and B in Fig. 4.1). There was at least a 1 m distance between plots in the same habitat (see C in Fig. 4.1). The stem length of each seedling was measured to the nearest centimetre from the stem base to the topmost leaf node before planting. The leaf litter layer was removed to expose a small area of soil and a small void was formed in the ground with a trowel. A seedling was planted up to the base of the stem and soil was pressed back around the seedling and the leaf litter layer was replaced. Nine seedlings were planted as evenly spaced as possible in each 1 m x 1 m plot (see D in Fig. 4.1).

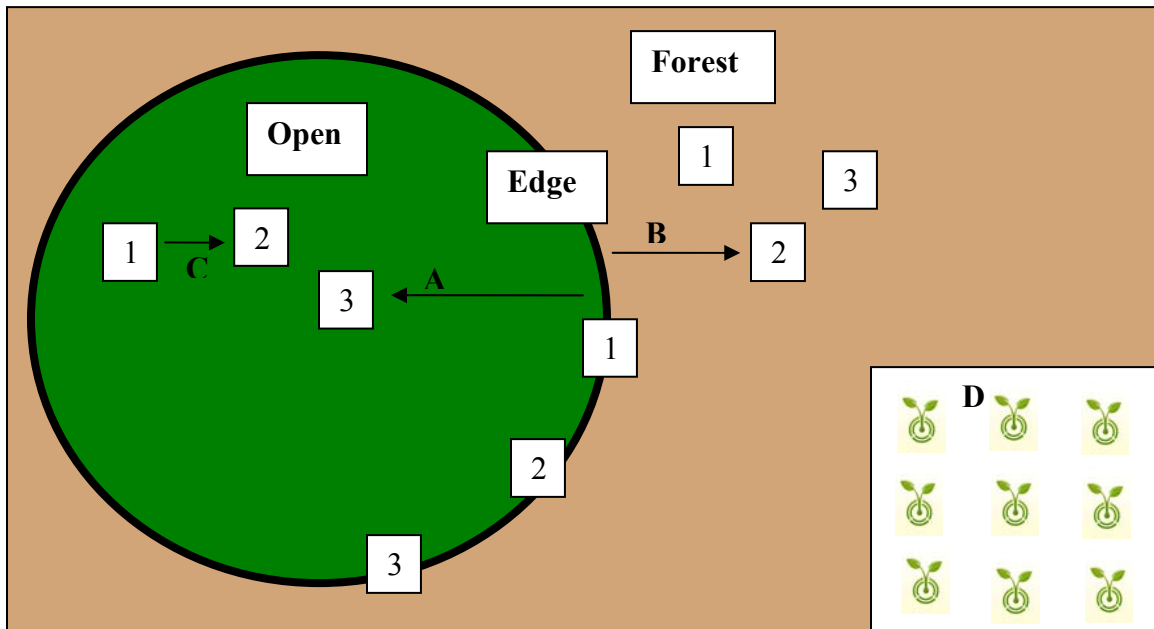


Fig. 4.1 The layout of seedling transplant plots and germination plots in three habitat types on Banks Peninsula in 2009-2010. Seedling transplant plots were set out at L'Aube Hill Reserve, Akaroa only. 1, 2 and 3 = 1 m x 1 m plots in a habitat type within which *C. vitalba* seedlings were planted.

On 18 January 2010, approximately 39 weeks after planting, the seedlings were removed from the site. Each seedling was logged as dead or alive, and all live seedlings were carefully removed from the soil with a trowel. The stem length of each seedling was remeasured to the nearest centimetre. Analysis was performed in R on both survival and growth data using the blocks of nine plants as replicates. The relative growth of each seedling was calculated by taking the natural log of the actual growth (final measurement minus initial measurement).

#### 4.2.3 Seedling emergence in the field

Mature seeds were collected from four *C. vitalba* vines at Sugarloaf and four *C. vitalba* vines at Reuter Reserve on 4 May 2009 and five *C. vitalba* vines at L'Aube Hill Reserve on 7 May 2009. About 13,000 seeds were collected in total and stored dry as a combined sample at room temperature for approximately two weeks. The white seed tails were removed from the seeds and the seeds were sorted into 248 sets of 50 seeds and stored dry in separate airtight plastic bags at room temperature for up to three weeks.

Three 1 m x 1 m seedling emergence plots were set out in three habitat types at Reuter Reserve and Sugarloaf on 2 June 2009 and at L'Aube Hill Reserve on 5 June 2009. The lay-out of plots at each site is the same as that for seedling transplants shown in Fig. 4.1. Again, open habitat plots were set out at least three metres from the edge of the forest and forest habitat plots were set out in the forest at least three metres from the forest edge. Within each plot, the leaf litter layer was removed completely and 18 plastic tubes, approximately 7 cm high with a diameter of 7.5 cm were set up in pairs relatively evenly spaced across the plot. The lay-out of seedling emergence tubes in each individual plot is shown in Fig. 4.2. Each tube was pressed into the soil approximately 1.0 to 1.5 cm, and then approximately 5 mm of the top soil layer from within each tube was removed. Within each pair of tubes, there was a manipulated tube and an unmanipulated tube. In the manipulated tube, the left tube of each pair, 50 *C. vitalba* seeds were spread in a single layer as evenly as possible on the soil. The right hand tube (unmanipulated) remained as it was, with no seeds added. Soil was replaced in both tubes and lightly compacted. To reduce disturbance from animals, falling debris and the weather, each pair of tubes was covered with wire mesh netting approximately 17 cm x 9 cm in size and secured to the ground with two metal pegs.



Figure 4.2 The set-up of 1 m x 1 m seedling emergence plots for *Clematis vitalba* in three habitat types at two sites on Banks Peninsula in 2009. Fifty *C. vitalba* seeds were sown in the left tube of each pair, and the right tube was unmanipulated, with no seeds added.

A final count of *C. vitalba* seedlings within each tube was made for Sugarloaf on 18 January 2010, for Reuter Reserve on 19 January 2010 and for L'Aube Hill Reserve on 21 January 2010, approximately 37 weeks after sowing. After the final count, all *C. vitalba* seedlings were removed from all seedling emergence tubes at all sites and destroyed.

#### 4.2.4 Glasshouse viability tests

To determine the viability of *C. vitalba* seed used above, 250 seeds from the combined seed sample were sown on 18 May 2009 and allowed to germinate. Five plastic pots approximately 15 cm high with a diameter of approximately 14 cm were filled with potting soil. In each pot, 50 seeds with their seed tails removed were sown evenly and to a depth



of approximately 5 mm. Each pot was covered with a layer of fine gravel to reduce the growth of *Marchantia* species. The pots were placed in a heated glasshouse with a daytime temperature of 20-22°C and a night-time temperature of 10-15°C for approximately four weeks and were watered daily. The pots were stored outdoors over winter from 7 July 2009 until 30 September 2009, when they were transferred back to the heated glasshouse. Seedling emergence was monitored on a weekly basis and *C. vitalba* seedlings were recorded and carefully removed with roots intact when they were large enough to identify. A final count of *C. vitalba* seedlings was taken on 13 January 2010, and the soil and any remaining seeds were disposed of.

#### **4.2.5 Statistical analyses**

Statistical analyses were performed in the statistical package R version 2.9.1. GLMs were used to estimate the influence of distance on seedling distribution, and to analyse the germination of *C. vitalba* seed and survival of planted seedlings. An analysis of variance (AOV) was used to analyse the growth of planted seedlings. All analyses were compared between habitat types and sites. A quasipoisson error distribution was fitted when needed to allow for overdispersion of the data. The fit of the AOV model was tested using an F test and the fit of all other models were tested using a Chi-square test.

### **4.3 RESULTS**

#### **4.3.1 Seedling distribution**

Twenty-three seedling distribution transects were completed and 19 of these encountered *C. vitalba* seedlings under 1 m in length. A total of 96 seedlings under 1 m were encountered; 59 occurred on the Port Hills and 37 were at Akaroa. Ten seedlings occurred in

the forest habitat and 22 in the open habitat at Akaroa, and 50 seedlings occurred in the forest habitat on the Port Hills and 14 were found in the open habitat on the Port Hills.

The number of seedlings varied between site and habitat type (Table 4.1). Habitat had a significant effect on the density of seedlings encountered during the distribution surveys. Distance and site were not significant, however, the interaction between site and habitat was significant. Akaroa contained a greater density seedlings in the open habitat, while the Port Hills was found to have more seedlings in the forest habitat (Fig. 4.3).

Table 4.1 Density of naturally occurring *Clematis vitalba* seedlings with a stem length of <1 m at two Banks Peninsula sites in 2009, from a poisson general linear model.

A: Analysis of Deviance Table

	DF	Deviance	Residual DF	Residual Deviance	P(> Chi )
NULL			689	407.46	
Site	1	3.35	688	404.11	0.07
Habitat	1	4.51	687	399.60	0.03
Distance	1	0.17	686	399.43	0.68
Site * habitat	1	15.54	685	383.89	<0.001
Site * distance	1	0.05	684	383.84	0.83
Habitat * distance	1	3.78	683	380.06	0.05
Site * habitat * distance	1	3.20	682	376.85	0.07

## B: Coefficients Table

	Estimate	Standard Error	Z value	Pr(> z )
(Intercept)	-1.73079	0.41733	-4.147	<0.001
Site - Port Hills	0.27260	0.51187	0.533	0.5943
Habitat - open	-0.89252	0.65261	-1.368	0.1714
Distance	-0.06152	0.03235	-1.901	0.0572
Site - Port Hills * habitat - open	-0.40396	0.90338	-0.447	0.6548
Site - Port Hills * distance	0.06642	0.03666	1.812	0.0700
Habitat - open * distance	0.10520	0.04131	2.546	0.0109
Site - Port Hills * habitat - open * distance	-0.09671	0.05445	-1.776	0.0757

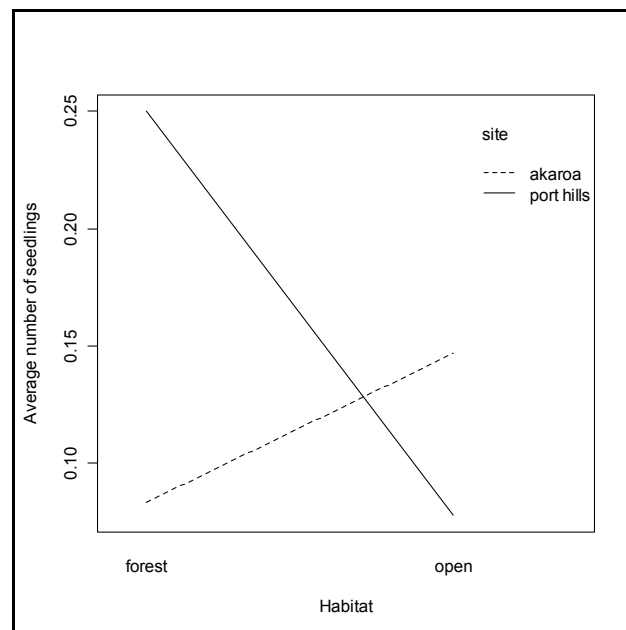


Figure 4.3 The average density per m<sup>2</sup> of naturally occurring *Clematis vitalba* seedlings with a stem length of <1 m in two habitat types at two sites on Banks Peninsula in 2009.

### 4.3.2 Seedling transplants

On 18 January 2010, 62 of the 81 *C. vitalba* seedlings planted at L'Aube Hill Reserve, Akaroa on 7 May 2009 were found to have survived. The survival of seedlings was greatest in the forest habitats (Fig. 4.4). Of the 27 seedlings planted in each habitat type, 93% survived in the forest, 74% survived out in the open and 63% survived at the edge. The average growth for the seedlings was 14.1 cm in the open habitats, 15.2 in the edge habitats, and 18.6 in the forest habitats; an average growth of 16.2 cm overall.

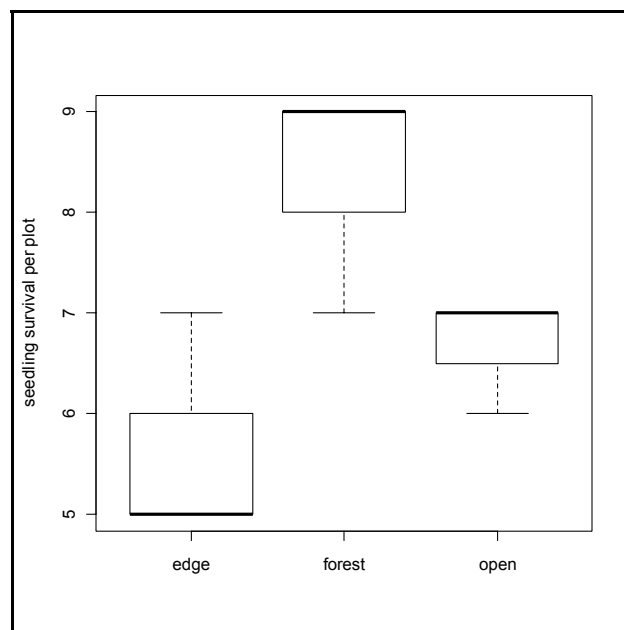


Fig. 4.4 A box and whisker plot showing the survival of planted *Clematis vitalba* seedlings in three habitat types in L'Aube Hill Reserve, Akaroa on Banks Peninsula between May 2009 and January 2010.

The survival of planted seedlings differed significantly between habitat type (Table 4.2A). Survival was greatest in the forest habitat (Table 4.2B). Habitat type also had a significant effect on the relative growth of planted seedlings (Table 4.3), where the relative growth was calculated by taking the log of the final measurement divided by the initial measurement of each seedling. Seedlings planted in the forest habitat had the greatest relative increase and seedlings in the edge habitat increased the least (Fig 4.5).

Table 4.2 The survival of planted *Clematis vitalba* seedlings in three habitat types at L'Aube Hill Reserve, Akaroa on Banks Peninsula between May 2009 and January 2010, from a binomial general linear model.

A: Analysis of Deviance Table

	DF	Deviance	Residual DF	Residual Deviance	P(> Chi )
NULL			8	13.9207	
Habitat	2	7.4912	6	6.4295	0.0236

B: Coefficients Table

	Estimate	Standard Error	z value	Pr(> z )
(Intercept)	0.5306	0.3985	1.331	0.183
Habitat - forest	1.9951	0.8360	2.387	0.017
Habitat - open	0.5192	0.5930	0.875	0.381

Table 4.3 The relative growth of *Clematis vitalba* seedlings planted into three habitat types at L'Aube Hill Reserve, Akaroa on Banks Peninsula between May 2009 and January 2010, from a gaussian general linear model. The relative growth of transplanted seedlings was calculated by taking the log of the final measurement divided by initial measurement of each seedling.

A: Analysis of Deviance Table

	DF	Deviance	Residual DF	Residual Deviance	P(> Chi )
NULL			61	7.7158	
Habitat	2	0.8953	59	6.8205	0.0208

B: Coefficients Table

	Estimate	Standard Error	t value	Pr(> t )
(Intercept)	0.57807	0.11216	0.213	<0.001
Habitat - forest	0.25716	0.10688	2.406	0.0193
Habitat - open	0.02388	0.11216	0.213	0.8321

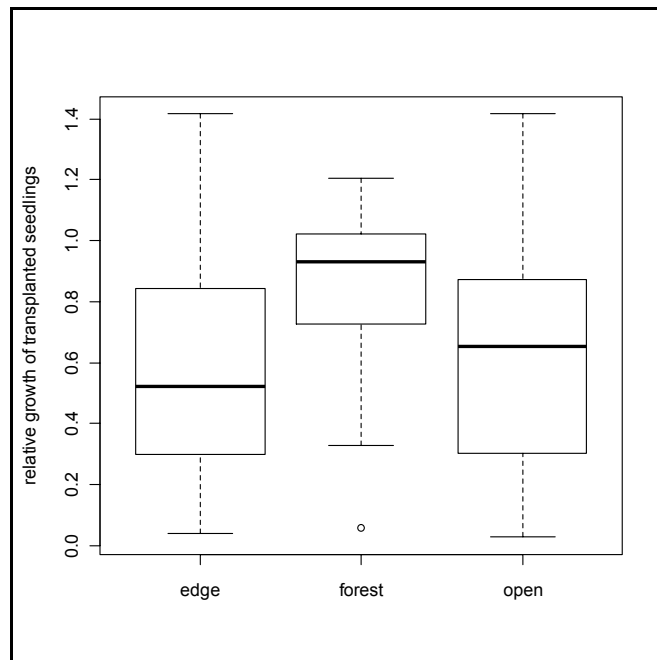


Figure 4.5 The relative growth of *Clematis vitalba* seedlings planted in three habitat types in L'Aube Hill Reserve, Akaroa on Banks Peninsula between May 2009 and January 2010. Also shown are the upper and lower quartiles (lines either side of the median), and whiskers encompassing 95% range of the data (designated by dashed lines), with an outlier that falls beyond the 95% range indicated by the open dot.

### 4.3.3 Seedling emergence

Between 2 June 2009 and 21 January 2010, 2120 *C. vitalba* seedlings germinated from a total of 12,150 seeds sown on Banks Peninsula. Seedling emergence was the highest at Akaroa (Fig. 4.6), with 1023 *C. vitalba* seedlings emerging across all habitats there, followed by 622 at Reuter Reserve and 475 at Sugarloaf, and 622. Overall, seedling emergence of *C. vitalba* seed was greatest in the open habitat (Fig. 4.7); there was a 38% germination rate in the open habitat, 6% germination in the forest habitat, and 8% germination in the edge habitat. The highest seedling emergence rate occurred in the open

habitat at Akaroa, with 62% of added seeds emerging there and the poorest seedling emergence rate occurred in forest habitat at Akaroa with 2% of added seeds emerging (Figure 4.8).

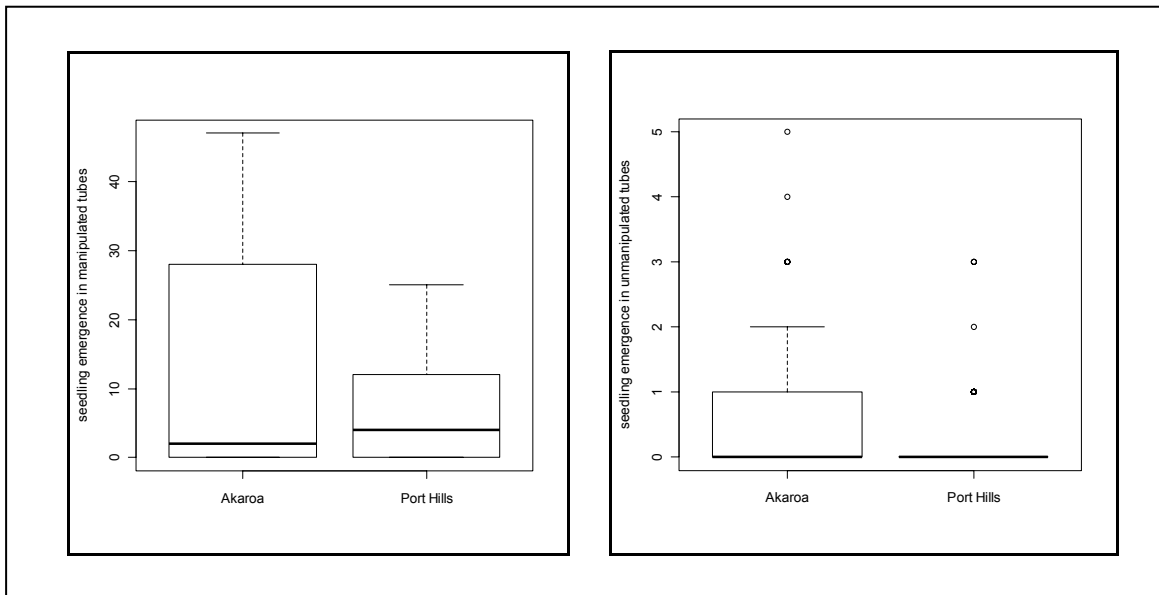


Figure 4.6 Variation in the emergence of *Clematis vitalba* seedlings from manipulated (50 seeds added) and unmanipulated (no seeds added) plots at two sites on Banks Peninsula between May 2009 and January 2010. Also shown are the upper and lower quartiles (lines either side of the median), and whiskers encompassing 95% range of the data (designated by dashed lines), with outliers that fall beyond the 95% range indicated by the open dots.



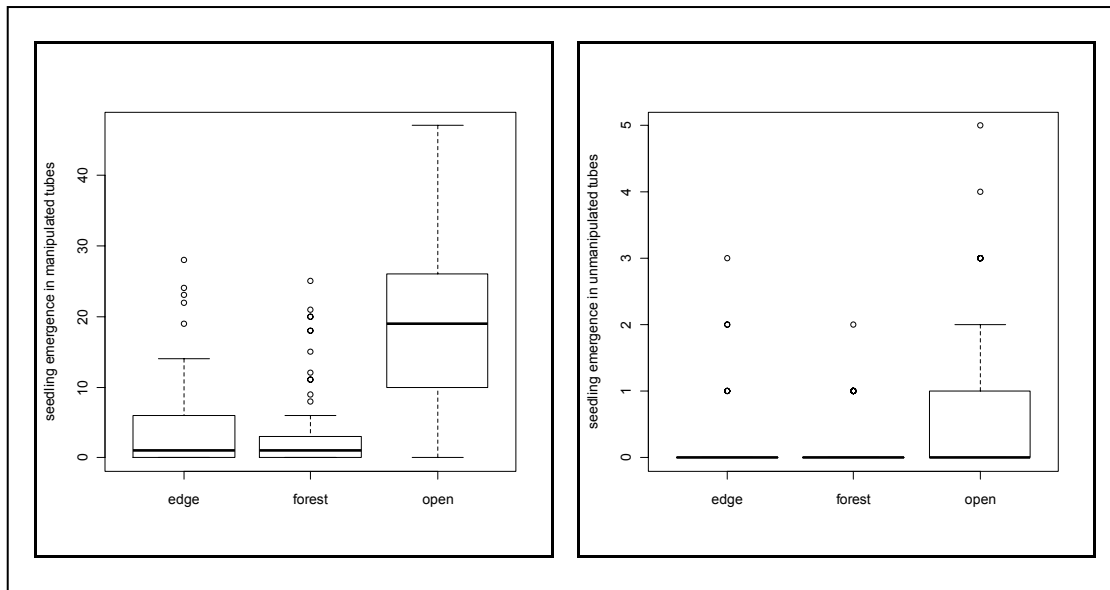


Fig. 4.7 Seedling emergence of *Clematis vitalba* from manipulated (50 seeds added) and unmanipulated (no seeds added) plots in three habitat types on Banks Peninsula between May 2009 and January 2010.

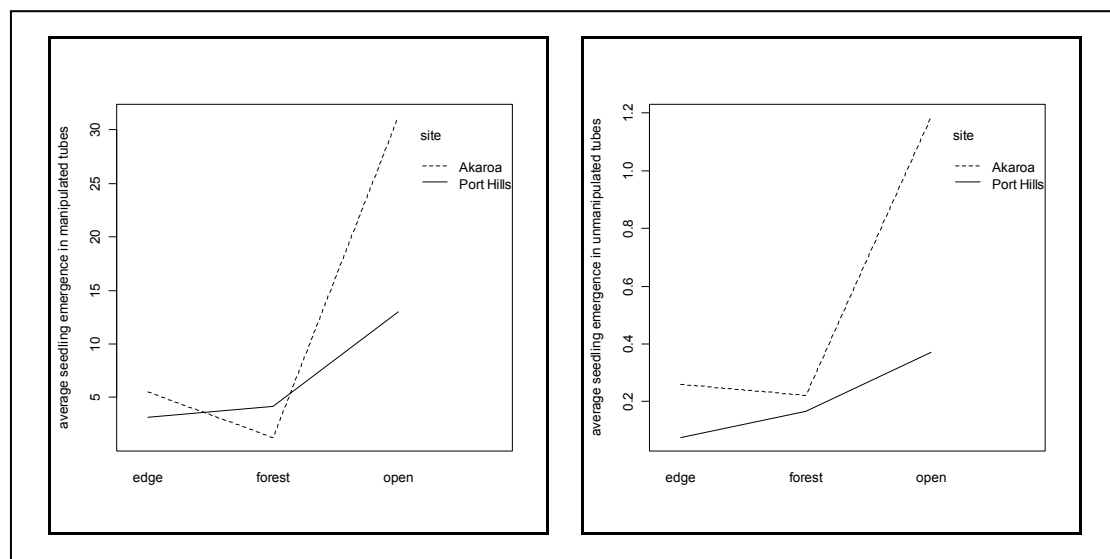


Fig. 4.8 The average seedling emergence of *Clematis vitalba* from manipulated (50 seeds added) and unmanipulated tubes (no seeds added) in three habitat types at two sites on Banks Peninsula between May 2009 and January 2010.

Over the same time period, a total of 78 *C. vitalba* seeds emerged in the unmanipulated condition; 58 % of seedling emergence occurred in Akaroa plots. Across all sites, the open habitat had the most seeds germinate in the unmanipulated condition. The open habitat at Akaroa elicited the greatest average number of seedlings, with an average of two *C. vitalba* seedlings emerging there and the forest habitat at Sugarloaf generated an average of 0.2 seedlings.

Habitat type and site had significant effects on the seedling emergence of *C. vitalba* (Table 4.4A). Seedling emergence was greatest in the open habitat. The seedling emergence of *C. vitalba* was also significantly different between manipulated and unmanipulated tubes.

Table 4.4 The seedling emergence of *Clematis vitalba* from seed added to three habitat types at two sites on Banks Peninsula between May 2009 and January 2010, from a quasipoisson general linear model.

A: Analysis of Deviance Table

	DF	Deviance	Residual DF	Residual Deviance	P(> Chi )
NULL			485	5849.3	
Habitat	2	1405.9	483	4443.4	<0.001
Site	1	214.6	482	4228.8	<0.001
Manipulated	1	2400.9	481	1827.9	<0.001
As factor (replication)	2	38.9	479	1789.0	<0.001
Habitat * site	2	171.0	477	1618.0	<0.001
Habitat * manipulated	2	4.2	475	1613.7	0.6
Site * manipulated	1	7.1	474	1606.6	0.2
As factor (replication) * as factor (tube no)	24	71.5	450	1535.1	0.8
Habitat * site * manipulated	2	6.4	448	1528.7	0.4

B: Coefficients Table

	Estimate	Standard Error	t value	Pr(> t )
(Intercept)	-1.78183	0.78957	-2.257	0.0245
Habitat - forest	-0.15415	1.09386	-0.141	0.8880
Habitat - open	1.51983	0.82039	1.853	0.0646
Site - Port Hills	-2.63906	2.10187	-1.256	0.2099
Manipulated - yes	3.05130	0.76050	4.012	<0.001
As factor (replication) 2	0.73924	0.32827	2.252	0.0248
As factor (replication) 3	0.38642	0.35000	1.104	0.2702
Habitat - forest * site - Port Hills	2.35138	2.34343	1.003	0.3162
Habitat - open * site - Port Hills	2.35138	2.17530	0.678	0.4978
Habitat - forest * manipulated - yes	-1.34655	1.15749	-1.163	0.2453
Habitat - open * manipulated - yes	0.21874	0.83890	0.261	0.7944
Site - Port Hills * manipulated - yes	2.13048	2.11322	1.008	0.3139
As factor (replication) 1 * as factor (tube.no) 2	0.33377	0.35380	0.943	0.3460
As factor (replication) 2 * as factor (tube.no) 2	-0.51988	0.30561	-1.701	0.0896
.....				
As factor (replication) 3 * as factor (tube.no) 9	0.14310	0.30416	0.470	0.6382
Habitat - forest * site - Port Hills * manipulated - yes	-0.60750	2.38194	-0.255	0.7988
Habitat - open * site Port Hills * manipulated - yes	-1.84375	2.18858	-0.842	0.4000

Glasshouse viability tests were performed on the *C. vitalba* seed collected from Banks Peninsula. Between 18 May 2009 and 13 January 2010, an average of 44% of the sown *C. vitalba* seeds germinated, with a standard error 3.58%.

## 4.4 DISCUSSION

### 4.4.1 Natural seedling distribution

*Clematis vitalba* seedlings were found growing in a range of conditions, from in the open under the parent plant to the shade of the canopy, far from the seed source. Bungard et al. (1997a) found that *C. vitalba* was associated with light levels >3% full sunlight, with 95% of occurrences in light levels that exceeded 5% full sunlight. Light levels >5% full sunlight are closely associated with forest margins and forest gaps (Bungard et al., 1997a). Light levels in undisturbed forest are most often between 1% and 3% full sunlight (Bungard et al., 1997a). The results obtained in this study are variable and are not consistent with these results of Bungard et al. (1997a); natural seedling distribution at the Port Hills was found to be closely associated with light levels between 1-3% full sunlight while the distribution observed at Akaroa was associated with higher levels of sunlight.

The variable results in the two habitat types at Akaroa and on the Port Hills could be due to a number of factors. There were differences in the landforms and species present in the open habitats at the two sites. The open habitat on the Port Hills contained mainly *P. cita* and exotic grasses with some areas of recently disturbed bare soil, while the open habitat at Akaroa contained mainly exotic grasses and *L. japonica* and there were no areas of bare soil. It is possible that the combination of vegetation and rocks may have limited the establishment and growth of *C. vitalba* seedlings. The open habitat on the Port Hills may have been grazed; there was no stock nearby for grazing to occur at Akaroa. While the site on the Port Hills is part of the reserve, it also borders on farmland, and it is possible that animals crossed the boundary fence into the reserve. If the area is grazed, that could explain the absence of seedlings in the open habitat on the Port Hills; *C. vitalba* is highly palatable to grazing animals and the species is practically absent within the browse tier in areas of Marlborough (Stein, 2004).

The presence of nutrients or gaps in the canopy in the forest on the Port Hills may have affected the presence of *C. vitalba* seedlings. According to Bungard et al. (1998), germination and growth of *C. vitalba* in response to light and nitrogen can account for the pattern of establishment in native forest remnants. It may be that the growth of *C. vitalba* seedlings is greater in a mixed-hardwood forest than under a canopy of *K. ericoides*. Also, the higher density of seedlings in the forest habitat on the Port Hills may have been due to the presence of waterways in the gully. Stein (2004) suggests that the reason *C. vitalba* is often found growing along waterways or at the bottom of gullies is because the presence of moisture is more reliable. Additionally, an unmeasured factor, such as climate or disturbance may have influenced natural seedling distribution. There may have been an unofficial or unrecorded period of herbicide or manual control of the species, but this seems unlikely to have successfully removed seedlings as control is usually concentrated on flowering plants.

#### **4.4.2 Seedling emergence**

Seed addition consistently enhanced seedling emergence at all three locations on Banks Peninsula; seedling emergence was greatest at Akaroa, with a total of 1023 *C. vitalba* seeds germinating there, and 622 seedlings and 475 seedlings emerging at Reuter Reserve and Sugarloaf respectively. It is possible that this seedling emergence pattern is related to climate; seeds added to habitats at Akaroa may have experienced a slightly warmer climate as L'Aube Hill Reserve is approximately 60 m.a.s.l., compared to approximately 150 m.a.s.l. for Reuter Reserve and 240 m.a.s.l. for Sugarloaf. Seedling emergence could also be explained by an unmeasured variable such as seed predation, pathogen attack, or seedling herbivory, or by the observed low germinability of the seed used in this study. The average seed germinability in this study was found to be 44%; Bungard et al. (1997a) found a higher average seed germination rate of 79%.

Seed addition also enhanced seedling emergence across all habitat types, however, the germination of *C. vitalba* in the open habitat was significantly greater than in the other two habitat types. A germination rate of approximately 31% was observed in the open habitat, 8% in the edge habitat, and 6% in the forest habitat. Bungard et al. (1997a) found that the germination of *C. vitalba* seed under laboratory conditions was affected by the level of light; they recorded a germination rate of about 70-80% in light and 40-60% in dark treatments. Although light influenced the final percentage of seedling emergence, the potential occurrence of this species is in both an open habitat and under a canopy. This allows *C. vitalba* to inhabit diverse environments, a characteristic which contributes to the success of this invasive species.

#### **4.4.3 Seedling survival and growth**

This study found an average increase of 16.2 cm in an eight-month period, a rate of approximately 24 cm per year for first-year seedlings. According to Gourlay et al., (1999) established *C. vitalba* vines can grow an average of 230 cm per year. The growth rate recorded in this study is far less than that; it is possible that conditions which promote rapid growth were not met. It is also possible that the resources accumulated by seedlings were used mostly in establishment and survival, and that growth rates may increase in the second year.

Previous studies (Bungard et al., 1997a; West, 1992) found that *C. vitalba* establishes better in habitats where elevated light levels occur. It is interesting then, that this study found that *C. vitalba* seedlings planted in forest habitats at Akaroa not only had the greatest rate of survival but also the greatest relative increase in stem length. Baars and Kelly (1996) found that *C. vitalba* had a greater degree of shade tolerance than previously reported, with a survival rate of 75% at 2% RI compared with 95% at higher light levels. Another introduced vine species in New Zealand, *Passiflora mollissima*, also has a light compensation point of around 2% RI (Baars and Kelly, 1996). However, *C. vitalba*

seedlings are less light demanding than seedlings of *Passiflora mollissima* and *P. pinnatistipula*, as they establish and reach the canopy in much less disturbed forest (Williams and Buxton, 1995). This may be partly due to a more vigorous growth of *C. vitalba* seedlings, a 'trellis search' strategy, rather than a 'sit and wait' strategy where growth is limited until suitable conditions occur (Williams and Buxton, 1995).

The survival of seedlings can be impacted by weather conditions. A study by Gómez-Aparicio (2008) found that seedling survival varied greatly between years, from about 20% in dry years to more than 50% in wet years. The positive effect of rainfall allowed a high percentage of seedlings from that year to survive their critical first summer. The authors also found that in dry years, survival was highest under established vegetation while in years of high rainfall, shrub understories were one of the least suitable microhabitats for survival. It is possible that in this study, weather conditions, or at least, the availability of water, affected the survival and growth of seedlings. Perhaps the year of this study was a 'dry year' which resulted in a lower growth rate of seedlings in open microsites, and the growth rate of approximately 24 cm per year.

## **CHAPTER 5 – Overall discussion**

### **5.1 Introduction**

As outlined in Chapter 1, seed limitation and establishment limitation are not mutually exclusive. A continuum exists, where at one extreme, populations are seed limited, and at the other end, population distributions are wholly influenced by the quality of available microsites. This chapter discusses the evidence found for seed limitation and microsite limitation in *C. vitalba* on Banks Peninsula and suggests the circumstances when each is likely to have a larger effect on population abundance and distribution. Directions for future research are suggested and implications for management and biological control are discussed with reference to seed and microsite limitation.

### **5.2 Summary of results**

The effect of habitat on seed and microsite limitation can be found in Table 5.1. Generally, Akaroa had a greater number of seeds dispersed, which is also reflected in the larger seed bank. Seedlings did best in sheltered habitats (forest and edge), while germination was much higher in the open habitats. Thus, the definition of an ideal habitat or microsite for *C. vitalba* depends on what life stage is under consideration. These contrasting effects could help explain why naturally occurring seedlings were more abundant in different habitats at the two sites. When considering both seedling emergence and survival of *C. vitalba* together, open habitats are ideal. Seedling emergence in open habitats was over 20 times that in forest habitats; and while seedling survival was greatest in the forest, the resulting seedling density from emerging seedlings would still be greater in the open.



The effect of distance on seed and microsite limitation is shown in Table 5.2. A slight distance effect was found for seed dispersal, but distance did not significantly affect the seed bank or the natural distribution of seedlings. This suggests that within 30 m of large seeding parent plants, dispersal is highly effective and seeds reach most microsites, therefore, seedling distribution is microsite limited not seed limited.

Table 5.1 Summary of the results of the effect of habitat from Chapters 3 and 4 showing the average result for each experiment. Values are rounded to the nearest whole number, with the exception of those for seedling distribution, as values of less than one are involved. A dash indicates that a particular experiment was not carried out under those conditions. NS = not significant, S = significant.

		Akaroa			Port Hills			Effect		
		Forest	Edge	Open	Forest	Edge	Open	Habitat	Site	Habitat * Site
<b>Seed Limitation</b>	<b>Seed dispersal</b> (seeds / 623.7 cm <sup>2</sup> / 23 weeks)	144	-	32	20	-	17	S	S	NS
	<b>Soil seed bank</b> (seedlings / kg)	8	-	2	1	-	0	S	S	NS
<b>Microsite Limitation</b>	<b>Seedling distribution</b> (seedlings / m <sup>2</sup> )	0.08	-	0.15	0.26	-	0.07	S	S	S
	<b>Seedling survival</b> (after 39 weeks)	93%	63%	74%	-	-	-	S	-	-
	<b>Seedling growth</b> (cm / 39 weeks)	19	15	14	-	-	-	S	-	-
	<b>Seedling emergence</b> (37 weeks)	2%	10%	60%	8%	6%	26%	S	S	S

Table 5.2 Summary of the results from Chapters 3 and 4 showing the effect of distance on the average result for each experiment. Values are rounded to the nearest whole number, with the exception of those for seedling distribution, as values of less than one are involved. A dash indicates that a particular experiment was not carried out under those conditions. NS = not significant, S = significant.

		Akaroa				Port Hills				Effect	
		0 m	10 m	20 m	30 m	0 m	10 m	20 m	30 m	Distance	Distance * Site
<b>Seed Limitation</b>	<b>Seed dispersal</b> (seeds / 623.7 cm <sup>2</sup> / 23 weeks)	122	97	66	52	47	10	12	6	S	NS
	<b>Soil seed bank</b> (seedlings / kg)	8	2	2	7	<1	<1	<1	0	NS	NS
<b>Microsite Limitation</b>	<b>Seedling distribution</b> (seedlings / m <sup>2</sup> )	0.36	0	0	0.55	0.25	0.17	0.17	0.42	NS	NS

### 5.3 Limitation in populations of *Clematis vitalba*

*Clematis vitalba* is adapted for highly efficient dispersal of its seed spatially and there is evidence of some temporal dispersal also. Long distance dispersal (LDD) and the seed bank play different roles in population recruitment. The extended tail of dispersal means that the species is likely to be less seed limited than expected, and LDD is important in the range expansion of this species. Long-lived, large seed banks should decrease the magnitude of seed limitation because viable seeds in the soil accumulate over time and can recruit into the population even in the absence of a productive seed year (Clark et al., 2007). Some temporal dispersal will decrease the magnitude of seed limitation, however, it would probably only have an effect in the short-term (1-2 years). *Clematis vitalba* can maintain a relatively constant, if small, soil seed bank through the combined strategy of high reproductive potential and seed dormancy. In this case, the seed bank provides its greatest adaptive importance during one or two growing seasons and aids recruitment in established populations.

According to Clark et al. (2007), the most direct approach to testing the relative importance of seed and microsite limitation for a species is to conduct seed addition tests. An increase in seedling density after seed addition indicates that a particular microsite is actually suitable for recruitment, and it can be concluded that limitations on species presence and/or abundance are at least partially attributable to seed limitation (Clark et al., 2007). In my study, the addition of *C. vitalba* seed to open, edge and forest habitats saw a significant increase in seedlings in all three habitats types. Thus, the population distribution and abundance of *C. vitalba* on Banks Peninsula is partially limited by seed dispersal.

The period between seed germination and seedling establishment is one of the most vulnerable transitions in the life cycle of plants (Gómez-Aparicio, 2008). The suitability of a microsite for recruitment might change between the seed, seedling and adult life stages (Schupp, 1995). If this is the case, then a bottleneck for recruitment will occur,

and the number of adults recruited into the population will be lower than the number of recruits observed shortly after germination (Baeten et al., 2009). As microsite preference for germination and seedling growth in *C. vitalba* changed between life stages, this change in microsite suitability between life stages could explain the differences observed. My study found that seedling emergence occurred in at least 89% of microsites and survival of planted seedlings was 55% or greater, yet natural seedlings were not encountered at most data collection points and average distribution was low (up to 0.5 seedlings per m<sup>2</sup>). It can be concluded that the conditions for seedling emergence are not as stringent as those for the establishment of plants.

As early recruitment stages are especially variable (Clark et al., 1999), samples across multiple years and multiple populations are required to assess the role of recruitment limitation. Other studies have found seedling survival to be patchy (Houle, 1992); the most favourable sites for seedling establishment are often unpredictable in time and space, and chance may play a significant role in seedling emergence and seedling survival. Future research should compare the survival rates of seedlings between different life stages of *C. vitalba*. Future studies should monitor seedlings to determine whether individuals reached maturity; are site conditions suitable for both seedling emergence and successful seedling establishment? To determine this, the survival of early seedlings and that of second- and third-year seedlings should be observed.

#### **5.4 How does limitation affect established and expanding populations of *Clematis vitalba*?**

Seed and microsite limitation are expected to vary over spatial scales relevant to dispersal because seeds are rarely, if ever, dispersed uniformly from the parent plant (Swope and Parker, 2010). Microsite limitation is often observed near the parent plant and seed limitation becomes more pronounced at increasing distance from the seed source (Fig. 5.3) (Clark et al., 2007; Poulsen et al., 2007). Established populations are more likely to be limited by the availability of microsites; both seed production and plant density is high

and environmental conditions are favourable (Swope and Parker, 2010). Recruitment may be microsite limited even where adult plant density is low if environmental conditions are suboptimal. Expanding populations will always be seed limited at the edge where current population density goes from low to zero (Swope and Parker, 2010). In contrast, seed limitation may be widespread in expanding populations or in populations under intensive control regimes (McAlpine and Jesson, 2008; Swope and Parker, 2010). Invasive species spread from ongoing long-distance dispersal and from short distance dispersal with lateral expansion of established populations (Sakai et al., 2001). Continued spread of established *C. vitalba* populations occurs because of excellent adaptations for dispersal.

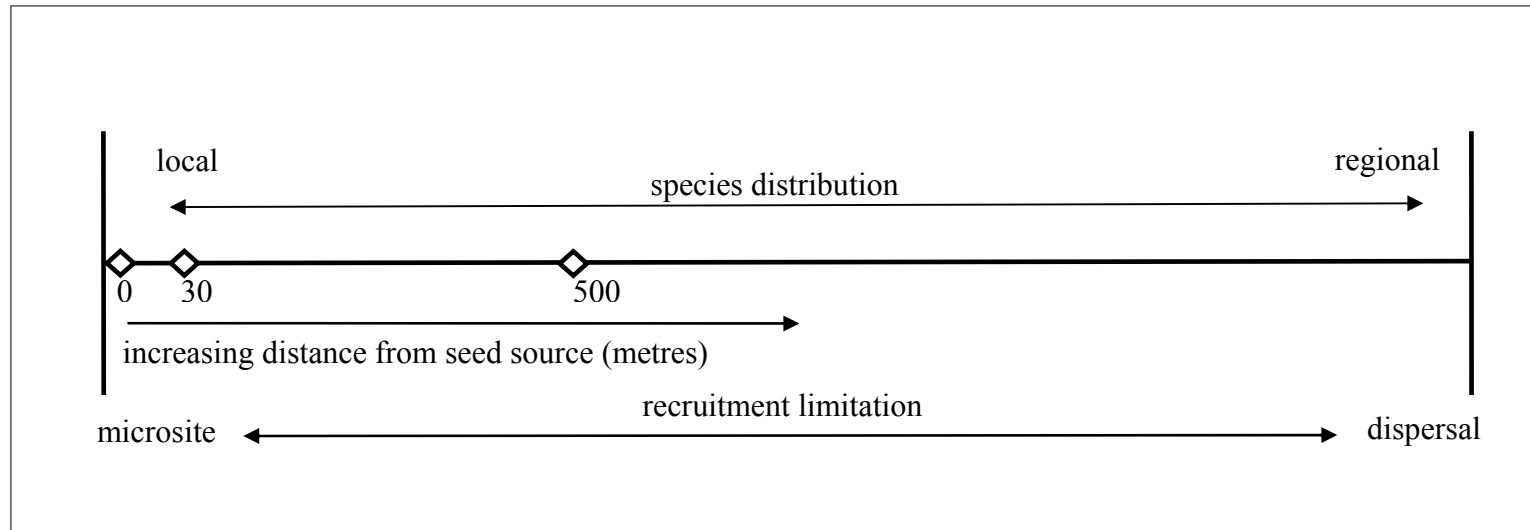


Fig. 5.1 A schematic representation of limitation in *Clematis vitalba* populations on Banks Peninsula. Near the seed source, where seed rain is high, microsite limitation plays the greatest role in the recruitment of individuals, while dispersal limitation is of greater importance.

## 5.5 Implications for management of *Clematis vitalba*

The management implications of this research are noteworthy. Seed dispersal of *C. vitalba* is highly efficient, thus the primary aim of control should be to remove all seed sources, and then prevent younger plants from producing seed. Suppressing seed production would be effective in preventing the persistence of a seed bank (Richardson and Kluge, 2008). Control should also aim to encompass an area of at least 500 m from the seed source(s) as I found seeds to be dispersed at least over this distance.

The confirmation of the presence of a small soil seed bank which persists for at least one year means that control and/or removal of seedlings in an affected area must continue for at least 12 months after removal of the seed source(s). Additional research into the survival of seed in the soil between 2-5 years would be beneficial as it would provide a more accurate time period for control. Stein (2004) suggests that *C. vitalba* in South Marlborough can be controlled by the presence of domestic stock (cows and sheep). Grazing may impact on the density of young seedlings, but it is unlikely to affect mature, woody vines; it may well be a useful technique for removing seedlings that have germinated from the soil seed bank.

Future biological control of *C. vitalba* should consider the magnitude of seed and microsite limitation in populations. The effects of a seed predator would be impacted by the degree of seed or microsite limitation within a population; a seed limited population would be much more sensitive to losses to seed predators (Swope and Parker, 2010). Seed predation could have a significant impact in expanding populations, because those populations will be seed limited at the edge of their range, but would have, however, a minimal impact on established populations where plant density is high.



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