

Linking seed dispersal, germination and seedling recruitment in the invasive species *Berberis darwinii* (Darwin's barberry)

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Abstract Seedling recruitment is a multi-phased process involving seed production, dispersal, germination, seedling establishment and subsequent survival. Understanding the factors that determine success at each stage of this process is of particular interest to scientists and managers seeking to understand how invasive species spread and persist, and identify critical stages for management. To understand the factors and processes influencing recruitment of the invasive species *Berberis darwinii* Hook. (Darwin's barberry), temporal and spatial patterns of seed dispersal, germination and seedling establishment were examined. Seed dispersal from a large source population was measured over two fruiting seasons, and subsequent patterns of seedling emergence and survival within each cohort were measured. Seed longevity was tested under both natural and artificial conditions. Seeds were widely dispersed by birds, up to 450 m from the source

population. Dispersal was essential to seedling establishment, as few seedlings survived beneath the parent canopy. Seeds were relatively short-lived in the soil under both field and glasshouse conditions, with few surviving for more than 1 year. Patterns of newly emerged seedlings largely reflected patterns of seed rain, but seedling survival was significantly affected by distance from source population, seedling density and light environment. These results suggest that recruitment of *B. darwinii* is dependent on dispersal of seeds to favourable microsites. Management priorities should include the removal of fruiting plants, and seedling control in highlight areas.

Keywords Invasion success · Invasive species management · Microsite limitation · New Zealand · Seed bank · Seedling establishment

Introduction

Seed dispersal, germination and seedling establishment are key processes influencing the abundance and distribution of plants. The likelihood of a propagule surviving each of these life stages may vary both spatially and temporally, and may depend on many factors (Schupp 1988; Houle 1998). Accordingly, it can be difficult to link the stages, and thus “map” the recruitment process (Howe et al. 1985; Jordano and Herrera 1995). Nevertheless, this is invariably an informative exercise, since the

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mechanisms underlying seedling establishment influence such a wide range of processes, from interspecific competitive interactions to general population dynamics. This information is particularly useful to have for invasive species because it can facilitate effective management programmes and accurate prediction of future range expansion. While seedling establishment in some species can be predicted largely by the number of seeds dispersed (Seidler and Plotkin 2006; Kollmann et al. 2007), in many species microsite availability limits establishment, and thus the spatial pattern of seed dispersal is partially or completely decoupled from the spatial pattern of seedling recruitment (Houle 1992; Schupp 1995; Rey and Alcàntara 2000).

The initial stage of seedling recruitment (following seed production) is seed dispersal. Dispersal is generally considered an adaptation to increase the probability of survival of offspring, but causative factors can be difficult to identify. The two main hypotheses that seek to explain the selective advantage of dispersal are: (i) escape from density-dependent competition and sources of parental-associated mortality (Janzen 1970; Connell 1971), and (ii) colonization of new sites that are unpredictable in time and space (Howe and Smallwood 1982). Seed dispersal also influences recruitment because it determines the physical environment that seeds and seedlings experience, which in turn affects survival (Schupp 1988; Wenny 2001). Weed species are frequently well-adapted for the efficient dissemination of their seed (Timmins and Mackenzie 1995; Binggeli 1996) and dispersal by any vector can result in widespread and prolific seed-deposition, and thus enhance the chances of invasion success (Lonsdale 1993; Williams and Karl 1996; Panetta and McKee 1997).

Following dispersal, seeds either germinate, die or are incorporated into the soil seed bank where they can remain dormant for months, years or even decades (Thompson et al. 1997). Seed banks can be usefully classified into three broad groups (cf. Bakker et al. 1996): (i) transient, where seeds persist in the soil for less than 1 year, often much less; (ii) short-term persistent, where seeds persist for at least 1 year, and up to 5 years; and (iii) long-term persistent, where seeds persist for more than 5 years. Many invasive species are early colonizers associated with ephemeral or unpredictable environments (Hobbs and

Hueneke 1992; Rejmánek 1995), but not all have persistent seed banks (Timmins and Williams 1987; Clement and Foster 1994). The life of the 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 (Panetta 2004; Panetta and Timmins 2004).

Seed and seedling survival are influenced by a virtually infinite array of ecological variables (Harper 1977; Howe 1989), and sites favourable for germination are not necessarily favourable for seedling establishment (Jordano and Herrera 1995; Schupp 1995; Figueroa and Lusk 2001). By comparing the spatial pattern of the seed rain with newly germinated seedlings and, later, with surviving seedlings, the environmental factors influencing final recruitment patterns can be determined. For example, Houle (1996) found that spatial patterns of seeds in the seed bank and emerging seedlings were not related to one another for either of two herbaceous species studied, and concluded that spatial patterns of recruitment were largely determined by factors influencing mortality at the germination stage. In a similar study of a shrub species, Rey and Alcàntara (2000) found that frugivore-generated dispersal patterns differed from the final pattern of recruitment because water-stress caused high mortality at the seedling stage. Understanding the factors that limit or promote seedling recruitment in a particular invasive species can be critical in determining why that species is invasive and where it is likely to invade.

The purpose of this study is to further understand the recruitment dynamics of an invasive species in New Zealand: *Berberis darwinii* Hook. (Berberidaceae) (Darwin's barberry). *Berberis darwinii* is a woody, evergreen, bird-dispersed shrub that grows to approximately 4 m high, native to southern Chile and Argentina. Initially brought to New Zealand as a garden plant, it was first recorded as naturalized in 1946 (Sykes 1982). It has since invaded many vegetation types throughout the country, including remnant forest stands, scrub and along roadsides (Webb et al. 1988), but little is known of its seed and seedling ecology. *Berberis darwinii* flowers in spring (Aug–Nov) and fruits in summer (Dec–Feb) in New Zealand, although both fruits and flowers can be found on plants almost year-round (Webb et al. 1988). Seed germination occurs in the spring

following dispersal (Allen and Wilson 1992). Anecdotal evidence suggests that it has a transient seed bank, but this has not previously been tested. It is also widely assumed that, since adult plants are shade tolerant, seedlings will be too. However, *B. darwinii* is a species of disturbed forest habitats in its native range (Landrum 1999), so this may not be true. In order to understand what factors influence recruitment—and thus invasion success—of *B. darwinii*, patterns of seed dispersal, seed longevity and seedling establishment were examined to answer the following question: What are the temporal and spatial patterns of *B. darwinii* seed dispersal and germination, and how do they relate to patterns of seedling establishment?

Methods

Study area

This study was conducted within the Karori Wildlife Sanctuary (KWS), a 249-ha ecological restoration site in Wellington, New Zealand (41°18.3' S, 174°44.8' E). Mean annual rainfall is 1,235 mm, and mean annual temperature is 12.8°C (16.9°C mid-summer and 8.8°C mid-winter) (Greater Wellington Regional Council 2005; National Institute of Water and Atmospheric Research 2005). The predominant vegetation is regenerating native podocarp/broadleaf forest, with remnant pockets of planted *Pinus radiata* D. Don and other exotic tree species (Moles and Drake 1999). A large stand (ca. 100 ha) of *B. darwinii* dominates the western hills adjacent to the KWS, and this is considered the source population for this study. Scattered *B. darwinii* plants do occasionally occur elsewhere within the KWS, but it is assumed that seed being dispersed from these plants is minimal compared to the quantity of seed being dispersed from the main source population, and is thus having little effect on the overall pattern of seed rain. Seed dispersal, germination and seedling establishment of *B. darwinii* was measured at a range of sites increasing in distance from this population (see below). In another study on *B. darwinii* in New Zealand, mean number of seeds per fruit was found to be 3.66 (s.d. 2.69, with a range of 1–14), and approximate number of fruit produced per adult plant estimated at 28,000

(Allen and Wilson 1992). Seeds range from 1.5–3 mm in length (Webb et al. 1988).

Seed dispersal

Berberis darwinii seed dispersal was measured at 10 locations for two consecutive summers: 2000–2001 and 2001–2002. Ten seed traps were placed at each of 10 locations increasing in distance from the source *B. darwinii* population: –10 m (directly below the source population canopy), 0 m (on the edge of the source population), 10, 25, 50, 100, 150, 250, 350 and 450 m. The first group of seed traps (–10 m) was distributed randomly beneath the source population canopy. The remaining groups of seed traps were laid out in lines approximately parallel to the canopy edge. In all cases, seed traps were placed a minimum of 3 m apart, with the base buried for stability.

Seed traps were made from plastic pots 150 mm high with a diameter of 200 mm. The base of each pot was replaced with a cotton liner for seed collection. Each seed trap sampled an area of 0.0314 m², so the total area sampled at each distance (10 seed traps per distance) was 0.314 m². The seed traps were set out in November 2000 and 2001 when fruits were beginning to mature. Liners were collected and replaced monthly until the end of the fruiting season (March 2001 and February 2002). Clean seeds that were free of fruit flesh were counted as bird-dispersed, while seeds that remained within an intact fruit were counted as gravity-dispersed. To estimate seed loss due to predation, intact fruits were placed in a subset of seed traps at each distance over the course of the experiment. These fruits were not damaged at all, so it was assumed that predators did not affect the number of fruit and seeds 'caught' in seed traps.

Seed longevity

The density and longevity of *B. darwinii* seeds in the natural seed bank was measured by taking soil cores at three monthly intervals between March 2001 and March 2002. Ten cores were taken from each of four locations increasing in distance from the source *B. darwinii* population (–10, 25, 250 and 450 m),

within 500 mm of a seed trap site. Soil core sites were covered with untreated cotton material after the first cores had been taken to prevent further seed rain input. Soil cores were cylindrical, 51 mm in diameter and 51 mm deep (including the litter layer). Each soil sample was passed through 10-mm mesh to remove stones and large roots, and was then spread out to a depth of 3–5 mm in a seedling tray containing a layer of peat. Trays were kept moist and exposed to natural day lengths in a neutrally shaded, unheated glasshouse. Control trays of sterile soil revealed no seed contamination. *Berberis darwinii* seedlings were counted, and removed as they emerged. Samples were last checked for germinated seedlings in January 2003.

As a further measure of the longevity of *B. darwinii* seed in the seed bank, bags of seeds were buried in the soil. *Berberis darwinii* fruits were collected in January 2001. Fruit pulp was removed, then seeds were air-dried for 3–7 days. Twenty-five seeds were placed in each of 44 small mesh bags made from 15 denier black nylon stockings. Bags of seeds were distributed evenly among four sites beneath the intact forest canopy at KWS, and were buried in the soil to a depth of approximately 50 mm. One bag was retrieved from each site every 3 months from May 2001 until February 2002, and then finally in August 2002. Once retrieved, seeds from each bag were sowed onto 30 mm of vermiculite, and were kept moist in a neutrally shaded, unheated glasshouse. Four replicates of 25 seeds were also sown fresh in January 2001. Seedlings were counted, and removed as they emerged for two germination seasons (spring) following seed sowing.

Germination and seedling survival

Natural seedling emergence and 5 month seedling survival were monitored for two seasons in forty 0.25 m² quadrats—ten at each of four locations increasing in distance from the source *B. darwinii* population (–10, 25, 250 and 450 m). Quadrats were established at the nearest suitable site adjacent to soil core locations. Newly emerged seedlings were counted after the peak germination period each year (November), then were re-counted and removed 5 months later.

Environmental measures

In order to establish the influence of light environment on seed germination and subsequent seedling survival, canopy openness was measured at all locations where natural germination and seedling establishment of *B. darwinii* were measured (10 sites each at –10, 25, 250 and 450 m from the edge of the source population), using a crown densiometer (Forestry Suppliers, USA). This instrument comprises a spherical, convex mirror, which reflects a large overhead area. A grid etched into the mirror is used to estimate the percentage of this overhead area covered by forest canopy (Lemmon 1957).

Statistical analyses

Data were analysed using S-Plus 4 (Mathsoft 1997) statistical software.

To examine differences in canopy openness at all locations where natural germination and seedling establishment of *B. darwinii* were measured (10 sites each at –10, 25, 250 and 450 m from edge of *B. darwinii* population), one-way ANOVA was used with site as predictor and canopy openness as response variable, followed by multiple pairwise comparisons. *P*-values of all post-hoc pairwise multiple comparisons are Bonferroni-corrected. For all ANOVA analyses and pairwise multiple comparisons, results, in which *P* < 0.05, are reported as significant.

In order to describe the seed dispersal curves for each year, two phenomenological models were fitted to the data using least squares regression: the negative exponential (linear in a semi-log plot), and inverse power law (linear in a log–log plot). To examine differences in the number of seeds dispersed to sites increasing in distance from the *B. darwinii* population, in two successive years, two-way ANOVA was used with site and year as predictors, and the number of seeds dispersed as response variable.

Factors influencing survival of two cohorts of naturally occurring seedlings were examined using generalized linear models, with a Gaussian distribution. The effect of seed rain density, seedling density, year, canopy openness and dispersal distance (predictors) on seedling survival (response variable) of

two seedling cohorts was tested, with seed rain density², seedling density² and canopy openness² added as predictors to check for any non-linear responses. Non-significant interactions were removed by stepwise removal (none was significant).

Results

Environmental measures

While locations for measuring natural *B. darwinii* germination and seedling establishment were selected solely on the basis of distance from source population, there were significant differences in canopy cover between them ($F = 10.14$, $P < 0.001$, $df = 3$). Canopy openness was highest at sites -10 m ($20 \pm 2\%$, mean ± 1 SE) and 450 m ($22 \pm 2\%$) sites, and lowest at 25 m ($11 \pm 0.9\%$) and 250 m ($10 \pm 1\%$) sites.

Seed dispersal

The total amount of seed dispersed differed by distance from source population and by year (Fig. 1, Table 1). There was also an interaction between distance and year (Table 1), with more seeds dispersed to middle-distance sites (10–150 m) in Year 1 (Fig. 1). The shape of the dispersal curve was similar for both years, with 92% of seeds falling directly beneath, or at the edge of, the source canopy, 6–7% dispersed within 100 m from the source, and the remaining 3–4% being dispersed up to 450 m away (Fig. 1). When only bird-dispersed seeds are considered, these percentages change to 65–76% of recovered seeds landing directly beneath, or at the edge of, the source canopy, 23–29% dispersed within 100 m from the source, and the remaining 1–5% being dispersed up to 450 m away. Gravity-dispersed seeds (fruits) were only found in seed traps located directly beneath *B. darwinii* plants (i.e. in the -10 and 0 m locations) (Fig. 1), but could potentially be dispersed further by rolling along the soil surface. The dispersal data best fitted an inverse power law model ($r^2 = 0.76$ in Year 1, $r^2 = 0.59$ in Year 2), which indicates a steep drop off in the curve near the source, but a more gradual drop off in the tail (Fig. 2), compared with the negative exponential model ($r^2 = 0.56$ in Year 1, $r^2 = 0.24$ in Year 2).

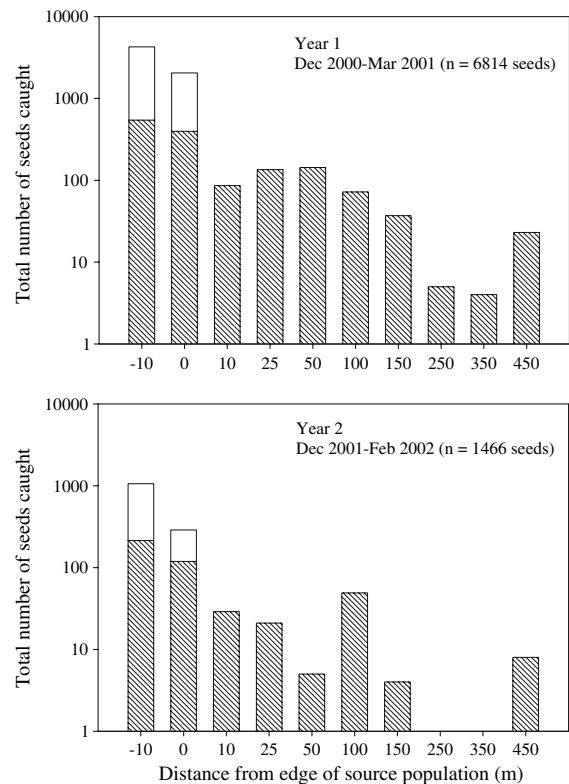


Fig. 1 Total number of *B. darwinii* seeds caught in seed traps at 10 sites increasing in distance from the source population during two fruiting seasons. White bars indicate gravity-dispersed seeds (still contained within the fruit), and shaded bars indicate bird-dispersed seeds (completely free of fruit pulp). Note y-axis is on a log scale

Seed bank dynamics

All three experiments investigating seed longevity (fresh seeds sown, seed burial and seed bank) indicated that only a small number of *B. darwinii* seeds survive for more than 1 year (Fig. 3). By far the majority of the viable seeds germinated during the first spring following seed production.

All germination from seed bank samples occurred in the spring following soil core extraction. However, few seedlings emerged from the seed bank samples (Fig. 3c). As expected, cores taken from directly beneath the *B. darwinii* canopy elicited the greatest number of seedlings, but this was still generally only between 1 and 3 seedlings per soil core (51 mm diameter \times 51 mm deep). Sites further away yielded none or very few seedlings per core, even from samples taken in March 2001, only 2 months after peak seed-fall (Fig 3c).

Table 1 Analysis of variance of *B. darwinii* seed dispersal by distance from source population and by year

Seed dispersal	Df	Dev	F	P
Distance	9	266.72	42.88	<0.001
Year	1	37.97	54.93	<0.001
Distance x Year	9	20.71	3.33	<0.001
Residuals	180			

Summary table indicates degrees of freedom (df), deviance (dev), variance ratios (*F*) and *P*-values (*P*)

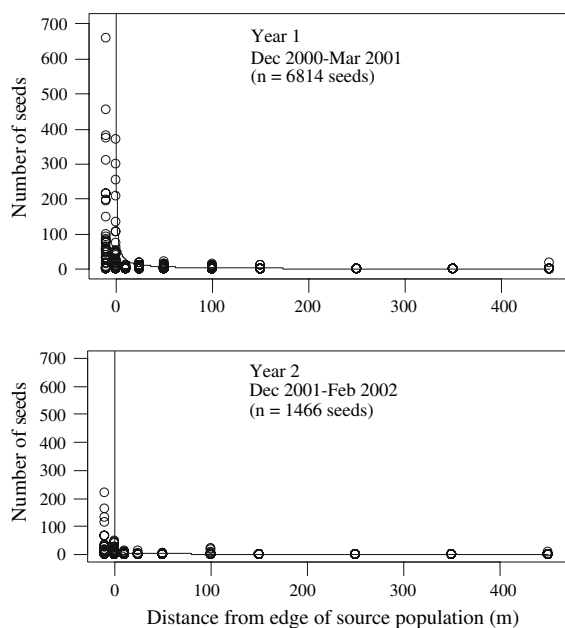


Fig. 2 Total number of *B. darwinii* seeds caught in each seed trap at 10 sites increasing in distance from the source population during two fruiting seasons. Lines indicate the predicted number of seeds dispersed using a negative exponential function. The predicted equations (taken from parameter values of General Linear Models) were Year 1: $\log(\text{Number}) = 5.230 - (0.830 \times \log(\text{Distance}))$; Year 2: $\log(\text{Number}) = 3.264 - (0.594 \times \log(\text{Distance}))$

Seedling establishment

Patterns of seedling emergence largely reflected patterns of seed dispersal, with density decreasing with distance from source population (Fig. 4). However, in the sites directly beneath the parent canopy, the total number of emergent seedlings differed in years, and differed in proportion to the total number of seeds produced: in Year 1, there were 135,796 seeds and 18,432 seedlings estimated per m^2 , while in

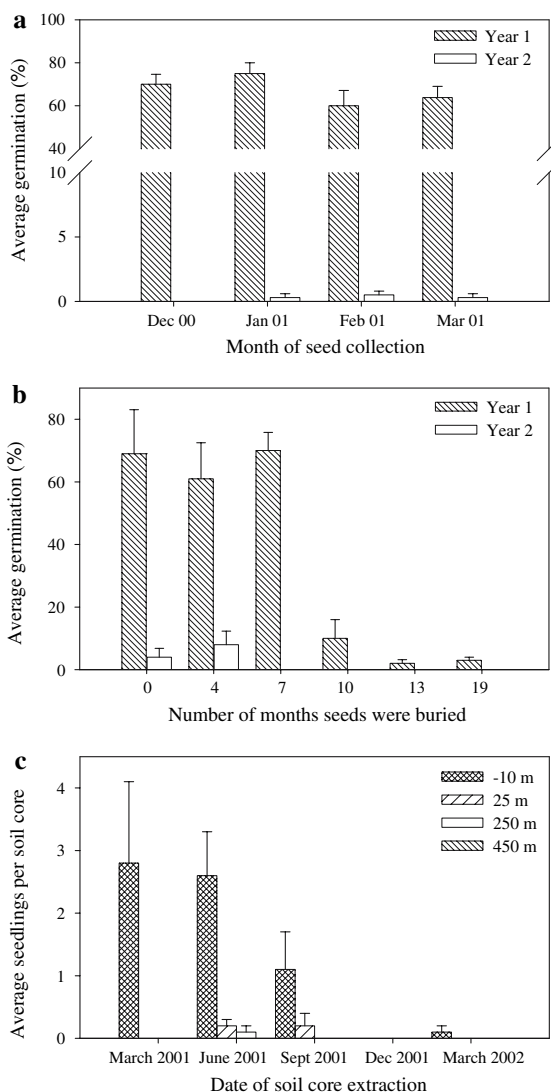


Fig. 3 Viability and longevity of *B. darwinii* seeds: (a) average percent germination of fresh seeds collected and sown monthly during the fruiting season of 2000–2001 ($n = 4 \times 20$ seeds sown per month), (b) average percent germination of seeds buried, then retrieved periodically over 19 months ($n = 4 \times 25$ seeds collected per date) and (c) average number of seeds germinated from soil cores collected periodically over the 12 months following the fruiting season of 2000–2001, from four sites increasing in distance from source population ($n = 10$ soil cores per distance, per date). For (a) and (b), germination was monitored for two germination seasons (= Year 1 and Year 2) following seed sowing, and for (c), germination was monitored for as long as seedlings continued to emerge, with the final check taking place in January 2003 (mean \pm 1 SE)

Year 2, there were 33,796 seeds and 9,796 seedlings estimated per m^2 . This also means that transition ratios differed in years: in Year 1, the ratio of seeds

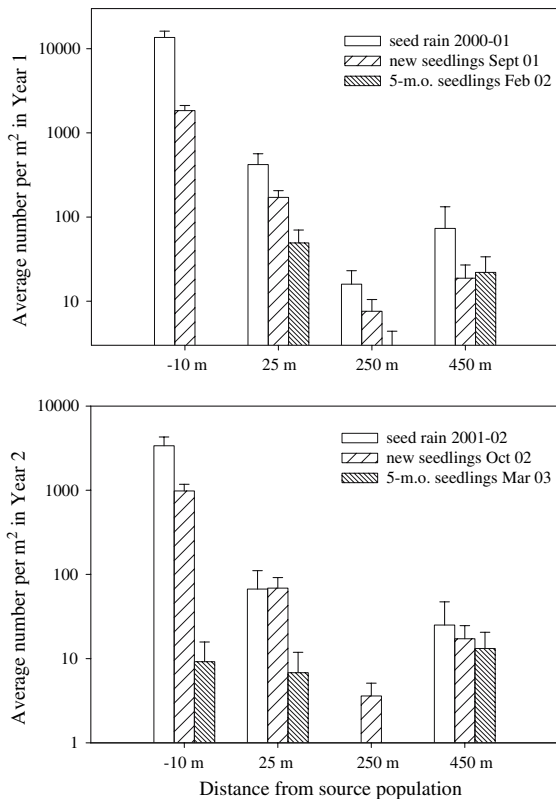


Fig. 4 Comparison of seed rain, newly emerged seedlings and 5 month seedling establishment in two cohorts of *B. darwinii*. Bars indicate the average number of individuals per m² in the seed rain (summer), of newly germinated seedlings (the following spring) and of approximately 5-month-old seedlings (the following summer) at four sites increasing in distance from the source population. For the seed rain $n = 10 \times$ seed traps per distance, and for seedlings $n = 10 \times 0.25 \text{ m}^2$ plots per distance (mean \pm 1 SE). Note y-axis is on a log scale

(in the seed rain) to seedlings was 7.4:1, but in Year 2, it was 3.5:1. Patterns appear to be similar in sites away from the parent canopy, with a greater proportion of the seed rain emerging as seedlings in Year 2 (Fig. 4).

Unlike seedling emergence, patterns of seedling establishment were uncoupled from patterns of seed dispersal, largely because few of the *B. darwinii* seedlings beneath the *B. darwinii* canopy survived (Fig. 5). Results indicate that survival of the two cohorts of naturally occurring seedlings was affected by all predictors considered: seed rain density, seedling density, year, canopy openness and distance from parent canopy (Table 2), but there were no interactions between variables. Distance—the predictor of most interest—was significant even after the

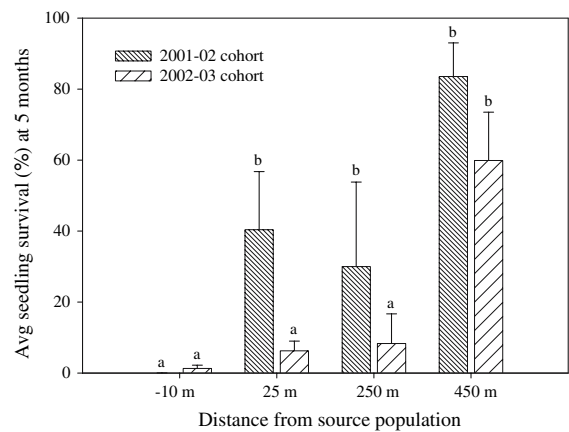


Fig. 5 Average percent survival of two cohorts of naturally occurring *B. darwinii* seedlings at increasing distance from the source population, 5 months after germination. Seedlings were surveyed in $10 \times 0.25 \text{ m}^2$ quadrats at each distance. Within each cohort, bars sharing the same letter are not significantly different from each other ($P < 0.05$) (mean \pm 1 SE)

variance explained by all other predictors had been accounted for. Seed rain² and seedling density² were also significant, indicating a non-linear response of survival to both seed rain density and seedling density. Seed rain density and distance explained the most variance ($P < 0.001$ in both cases, see Table 2), but these variables are likely to be highly correlated. Furthermore, the direction of the effect differed in these variables: survival was negatively affected by increasing seed rain density, but

Table 2 Generalized linear model of survival of two cohorts of naturally occurring *B. darwinii* seedlings by seed rain density, seedling density, year, canopy openness and distance from source population

Seedling survival	Df	Dev	F	P
Seed rain density	1	36.90	19.46	<0.001
Seed rain density ²	1	11.98	6.32	0.015
Seedling density	1	8.45	4.46	0.040
Seedling density ²	1	6.67	3.52	0.066
Year	1	16.54	8.72	0.005
Canopy openness	1	13.54	7.14	0.010
Canopy openness ²	1	0.13	0.07	0.795
Distance	3	38.14	6.70	<0.001

Seed rain density, seedling density and canopy openness were also squared in order to test for a non-linear response of seedling survival to density and canopy. Summary table indicates degrees of freedom (df), deviance (dev), variance ratios (F) and P-values (P)

positively affected by increasing distance from the source population (Figs. 4, 5). This probably explains why there was no interaction between density and distance.

Discussion

Successful weed invasion has been shown to be correlated with traits such as dispersal (Parendes and Jones 2000; Stansbury 2001) and prolific seed production (e.g. Scott 1996; Roche et al. 1997; Buist et al. 2000), however, site-specific factors will also determine invasion success. Here we show that microsite availability can limit invasion success in a bird-dispersed species, and we suggest that the interaction of microsite availability and dispersal ability needs to be taken into account in assessing invasion risk. In this study, dispersal of *B. darwinii* seeds to sites away from the parent population was crucial for seedling establishment, suggesting that widespread dispersal is a key trait in the invasive success of this species. A high number of seeds were dispersed up to 150 m from the parent population, and seeds were also consistently detected at distances up to 450 m away. A seed dispersal curve is generally assumed to be negatively exponential in shape (Howe 1986; Willson 1993), but in this study, it was best described by an inverse power function. This implies that the “tail” of the curve was more drawn-out than expected, which, in vertebrate-dispersed species, has previously been attributed to the ability of animals to transport seeds over long distances (Laman 1996; Panetta and Sparkes 2001). Long distance dispersal can accelerate the invasion process by initiating new “satellite” populations (Moody and Mack 1988; Kot et al. 1996), and is thought to be disproportionately important to a range of recruitment processes (Clark et al. 1998; Cain et al. 2000). Furthermore, *B. darwinii* can produce fruit by 2 years of age (KGM, pers. obs.), and fruits earlier in the season than many other plant species in New Zealand (Allen and Lee 1992). All of these factors support previous suggestions that *B. darwinii* is a prolific fruit producer with highly effective seed dispersal mechanisms (Allen and Wilson 1992).

Despite being a prolific seed producer, patterns of recruitment in *B. darwinii* were uncoupled from seed dispersal. *Berberis darwinii* seeds dispersed away from the source population had a much higher chance

of surviving at the seedling stage; almost all seedlings beneath the parent canopy died within the first 5 months following germination, in both study years (Fig. 4). Seedlings occurring at high densities commonly experience high mortality due to factors such as competition, the presence of pathogens, or allelopathic effects (Augspurger 1983b; Hulme 1998; Packer and Clay 2000), although there was no obvious cause in this study. Our analyses suggest that seed rain density, seedling density, and distance from source population play a role in this, although results were variable, and all factors are likely correlated. Other studies have found seedling survival to be patchy and inconsistently correlated with distance from source population—both within and between years (Whelan et al. 1991; Houle 1992). Thus the most favourable sites for seed dispersal are often unpredictable in time and space, and chance may play a significant role in seedling survival.

Having long-lived seeds can be advantageous for invasive species, because propagules are effectively dispersed in time, poised to take immediate advantage when changing conditions become favourable for germination (Panetta 2004). On the other hand, it may be equally advantageous to produce large amounts of short-lived seeds that germinate *en masse* in the spring, thus lessening the risk of prolonged exposure to seed predators and pathogens (Alvarez-Buylla and Martínez-Ramos 1990). Particularly when coupled with effective spatial seed dispersal, this strategy produces numerous, widespread seedlings at the time of year most conducive to seedling survival. Our results indicate that *B. darwinii* employs the latter strategy—almost all seeds germinate the first spring following dispersal, regardless of microsite conditions. This results in a carpet of seedlings that extends for hundreds of metres from the parent population (KGM, pers. obs.). The chances of at least some of these seedlings emerging in sites where conditions are suitable for establishment are likely high.

Prolific seed production alone does not necessarily increase recruitment, because there is likely to be an upper limit on the number of dispersers available, and on the number of seedlings that can emerge per unit area. In the sites directly beneath the parent canopy, there were four times as many seeds in Year 1 compared to Year 2. However, there were only twice as many newly germinated seedlings in Year 1 compared to Year 2, indicating that a larger

proportion of the crop emerged as seedlings in Year 2. This may be because sites were saturated with seed in Year 1, so the number of seedlings was limited by seedling competition and/or microsite availability. Conversely, a larger proportion of the crop in Year 2 also emerged as seedlings in sites less saturated with seed (sites at 25, 250, and 450 m from source population) (Fig. 3), suggesting that either a larger proportion of the crop was dispersed in Year 2, or that weather conditions were more favourable for germination. Several other studies have also shown that proportionally more of the fruit crop is taken by frugivores when a small crop is produced (Jordano 1987; Herrera 1998). Seed addition studies found that *B. darwinii* seeds germinate successfully in all light environments, but seedlings only establish in high light environments (McAlpine and Drake 2003; McAlpine and Jesson 2007). While the current study only measured survival to 5 months, and patterns of seedling establishment may change further, it seems likely that dispersal away from the population and microsite availability interacted to create the recruitment patterns seen.

Five months after germination, there was no strong relationship between seed rain and seedlings, likely due to density-dependant mortality and light environment. However, overall seedling survival in sites away from the parent canopy was generally higher in Year 1 than in Year 2 (Fig. 4), suggesting that higher fruit abundance (as indicated by higher seedfall) may increase recruitment under some circumstances. Certainly the quantity of fruit produced can vary significantly between years (Herrera 1998), but only long-term research can elucidate what effect this has on seedling recruitment.

In summary, successful recruitment of *B. darwinii* depends on the dispersal of seeds away from the parent canopy, to microsites in high light environments. Prolific seed production, and widespread seed dispersal are often considered key traits contributing to invasion success, but our results show that microsite availability can be equally important.

Management implications

Given the prolific and widespread nature of *B. darwinii* seed dispersal, removal of the seed source should be the initial management priority. However,

this is not always possible, and in many situations the aim of weed control is to control seedlings before they reach reproductive maturity. If frugivorous birds are present during the summer fruiting period, by spring, newly germinated seedlings are likely to be found up to 450 m away from the source population, in any type of habitat. However, seedlings beneath the parent canopy and in other shady environments will largely die out naturally, so seedling control in these areas is unnecessary. The seed bank is of minor concern, since most seeds do not last for more than 1 year.

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References

- Allen RB, Lee WG (1992) Fruit selection by birds in relation to fruit abundance and appearance in the naturalised shrub *Berberis darwinii*. N Z J Bot 30:121–124
- Allen RB, Wilson JB (1992) Fruit and seed production in *Berberis darwinii* Hook., a shrub recently naturalised in New Zealand. N Z J Bot 30:45–55
- Alvarez-Buylla E, Martínez-Ramos M (1990) Seed bank versus seed rain in the regeneration of a tropical pioneer tree. Oecologia 84:314–325
- Augsburger CK (1983b) Seed dispersal of the tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. J Ecol 71:759–771
- Bakker JP, Poschod P, Strykstra RJ, Bekker RM, Thompson K (1996) Seed banks and seed dispersal: important topics in restoration ecology. Acta Bot Neerl 45:461–490
- Binggeli P (1996) A taxonomic, biogeographical and ecological overview of invasive woody plants. J Veg Sci 7:121–124
- Buist M, Yates CJ, Ladd PG (2000) Ecological characteristics of *Brachychiton populneus* (Sterculiaceae) (kurrajong) in relation to the invasion of urban bushland in south-western Australia. Austral Ecol 25:487–496
- Cain ML, Milligan BG, Strand AE (2000) Long-distance seed dispersal in plant populations. Am J Bot 87:1217–1227
- Clark JS, Fastie C, Hurr G, Jackson ST, Johnson C, King GA, Lewis M, Lynch J, Pacala S, Prentice C, Schupp EW, Webb III T, Wyckoff P (1998) Reid's paradox of rapid plant migration: dispersal theory and interpretation of paleoecological records. BioScience 48:13–24
- Clement EJ, Foster MC (1994) Alien plants of the British Isles. Botanical Society of the British Isles, London
- Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain

- forest trees. In: den Boer PJ, Gradwell GR (eds) Dynamics of populations. Centre for agricultural publishing and documentation, Wageningen, The Netherlands, pp 298–312
- Figueroa JA, Lusk CH (2001) Germination requirements and seedling shade tolerance are not correlated in a Chilean temperate rain forest. *New Phytol* 152:483–489
- Greater Wellington Regional Council (2005) Rainfall data recorded at Karori Wildlife Sanctuary 1879–2004. Laura Watts, Greater Wellington Regional Council
- Harper JL (1977) Population biology of plants. Academic Press, London
- Herrera CM (1998) Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. *Ecol Monogr* 68:511–538
- Hobbs RJ, Huenneke LK (1992) Disturbance, diversity and invasion: implications for conservation. *Conserv Biol* 6:324–338
- Houle G (1992) Spatial relationship between seed and seedling abundance and mortality in a deciduous forest of north-eastern North America. *J Ecol* 80:99–108
- Houle G (1996) Environmental filters and seedling recruitment on a coastal dune in subarctic Quebec (Canada). *Can J Bot* 74:1507–1513
- Houle G (1998) Seed dispersal and seedling recruitment of *Betula alleghaniensis*: spatial inconsistency in time. *Ecology* 79:807–818
- Howe HF (1986) Seed dispersal by fruit-eating birds and mammals. In: Murray DR (ed) Seed dispersal. Academic Press, Australia, pp 123–189
- Howe HF (1989) Scatter- and clump-dispersal and seedling demography: hypothesis and implications. *Oecologia* 79:417–426
- Howe HF, Smallwood J (1982) Ecology of seed dispersal. *Annu Rev Ecol Syst* 13:201–228
- Howe HF, Schupp EW, Westley LC (1985) Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). *Ecology* 66:781–791
- Hulme PE (1998) Post-dispersal seed predation: consequences for plant demography and evolution. *Perspect Plant Ecol* 1:32–46
- Janzen DH (1970) Herbivores and the number of tree species in tropical forests. *Am Nat* 104:501–528
- Jordano P (1987) Avian fruit removal: effects of fruit variation, crop size, and insect damage. *Ecology* 68:1711–1723
- Jordano P, Herrera CM (1995) Shuffling the offspring: uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. *Ecoscience* 2:230–237
- Kollmann J, Frederiksen L, Vestergaard P, Bruun HH (2007) Limiting factors for seedling emergence and establishment of the invasive non-native *Rosa rugosa* in a coastal dune system. *Biol Invasions* 9:31–42
- Kot M, Lewis MA, van den Driessche P (1996) Dispersal data and the spread of invading organisms. *Ecology* 77:2027–2042
- Laman TG (1996) *Ficus* seed shadows in a Bornean rain forest. *Oecologia* 107:347–355
- Landrum LR (1999) Revision of *Berberis* (Berberidaceae) in Chile and adjacent southern Argentina. *Ann Mo Bot Gard* 86:793–834
- Lemmon PE (1957) A new instrument for measuring forest overstorey density. *J Forest* 55:667–668
- Lonsdale WM (1993) Rates of spread of an invading species: *Mimosa pigra* in northern Australia. *J Ecol* 81:513–521
- Mathsoft (1997) S-Plus 4 guide to statistics. Data Analysis Software Division. Mathsoft, Seattle, Washington, USA
- McAlpine KG, Drake DR (2003) The effects of small-scale environmental heterogeneity on seed germination in experimental treefall gaps in New Zealand. *Plant Ecol* 165:207–215
- McAlpine KG, Jesson LK (2007) Biomass allocation, shade tolerance and seedling survival of the invasive species *Berberis darwinii* (Darwin's barberry). *New Zeal J Ecol* 31:1–12
- Moles AT, Drake DR (1999) Potential contributions of the seed rain and seed bank to regeneration of native forest under plantation pine in New Zealand. *N Z J Bot* 37:83–93
- Moody ME, Mack RN (1988) Controlling the spread of plant invasions: the importance of nascent foci. *J Appl Ecol* 25:1009–1021
- National Institute of Water, Atmospheric Research (2005) National Climate Centre Database. Wellington, New Zealand
- Packer A, Clay K (2000) Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature* 404:278–281
- Panetta FD (2004) Seed banks: the bane of the weed eradicator. In: Proceedings of the Fourteenth Australian Weeds Conference, Wagga Wagga, pp 523–526
- Panetta FD, McKee J (1997) Recruitment of the invasive ornamental, *Schinus terebinthifolius*, is dependent upon frugivores. *Aust J Ecol* 22:432–438
- Panetta FD, Sparkes EC (2001) Reinvasion of a riparian forest community by an animal-dispersed tree weed following control measures. *Biol Invasions* 3:75–88
- Panetta FD, Timmins S (2004) Evaluating the feasibility of eradication for terrestrial weed incursions. *Plant Prot Q* 19:5–11
- Parendes LA, Jones JA (2000) Role of light availability and dispersal in exotic plant invasion along roads and streams in the HJ Andrews experimental forest, Oregon. *Conserv Biol* 14:64–75
- Rejmánek M (1995) What makes a species invasive? In: Pyšek P, Prach K, Rejmánek M, Wade M (eds) Plant invasions: general aspects and special problems. SPB Academic Publishing, Amsterdam, pp 3–13
- Rey PJ, Alcántara JM (2000) Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. *J Ecol* 88:622–633
- Roche CT, Thill DC, Shafii B (1997) Reproductive phenology in yellow starthistle (*Centaurea solstitialis*). *Weed Sci* 45:763–770
- Schupp EW (1988) Factors affecting post-dispersal seed survival in a tropical forest. *Oecologia* 76:525–530
- Schupp EW (1995) Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *Am J Bot* 82:399–409
- Scott JK (1996) Population ecology of *Chrysanthemoides monilifera* in South Africa: implications for its control in Australia. *J Appl Ecol* 33:1496–1508

- Seidler TG, Plotkin JB (2006) Seed dispersal and spatial pattern in tropical trees. *PLoS Biol* 4:2132–2137
- Stansbury CD (2001) Dispersal of the environmental weed bridal creeper, *Asparagus asparagoides*, by silveryeyes, *Zosterops lateralis*, in south-western Australia. *Emu* 101:39–45
- Sykes WR (1982) Checklist of dicotyledons naturalised in New Zealand 15. Annonales, Berberidales, Cactales, Fagales, some Geraniales, Juglandales, Laurales, Rurales, Salicales, Sapindales, Tiliales, Nyctaginaceae, and Zygophyllaceae. *N Z J Bot* 20:333–341
- Thompson K, Bakker JP, Bekker RM (1997) The soil seed banks of north west Europe: methodology, density and longevity. Cambridge University Press, Cambridge
- Timmins SM, Williams PA (1987) Characteristics of problem weeds in New Zealand's protected natural areas. In: Saunders DA, Arnold GW, Burbidge AA, Hopkins AJM (eds) Nature conservation: the role of remnants of native vegetation. Surrey Beatty and Sons Pty Limited, NSW, pp 241–247
- Timmins SM, Mackenzie IW (1995) Weeds in New Zealand protected natural areas database. Department of Conservation Technical Series No. 8. Department of Conservation, Wellington, New Zealand
- Webb CJ, Sykes WR, Garnock-Jones PJ (1988) Flora of New Zealand vol IV. Naturalised pteridophytes, gymnosperms, dicotyledons. Botany Division DSIR, Christchurch
- Wenny DG (2001) Advantages of seed dispersal: a re-evaluation of directed dispersal. *Evol Ecol Res* 3:51–74
- Whelan CJ, Willson MF, Tuma CA, Souza-Pinto I (1991) Spatial and temporal patterns of post-dispersal seed predation. *Can J Bot* 69:428–436
- Williams PA, Karl BJ (1996) Fleshy fruits of indigenous and adventive plants in the diets of birds in forest remnants, Nelson, New Zealand. *N Z J Ecol* 20:127–145
- Willson MF (1993) Dispersal mode, seed shadows, and colonization patterns. *Vegetatio* 107/108:261–280