



Survival rates of Darwin's barberry (*Berberis darwinii*) seedlings in mixed beech-broadleaf forest in New Zealand



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Survival rates of Darwin's barberry (*Berberis darwinii*) seedlings in mixed beech-broadleaf forest in New Zealand

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Abstract

Intact New Zealand podocarp-broadleaf forest is relatively resistant to invasion from Darwin's barberry (*Berberis darwinii* Hook. Berberidaceae), probably because low light conditions inhibit early seedling establishment. We investigate whether intact New Zealand beech-broadleaf forest is similarly resistant to invasion by Darwin's barberry. We measured canopy openness and counted young and older Darwin's barberry seedlings along transects leading into beech-broadleaf forest at four sites, first at peak germination time (November), then 5 months later (April). Young (<1 year-old) seedlings were most abundant near the forest edge, but were not strongly correlated with canopy openness. Young seedling survival was estimated to be 23%, which is higher than survival rates reported from New Zealand podocarp-broadleaf forest. However, older (>1-year-old) seedlings were strongly associated with the forest edge and higher light conditions. Accordingly, we conclude that Darwin's barberry probably cannot establish beneath an intact canopy of beech-broadleaf forest in New Zealand. However, forest edges and canopy gaps are likely to be susceptible to invasion.

Keywords: weed, invasive species, seedling establishment, light environment, canopy openness

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1. Introduction

Intact New Zealand podocarp-broadleaf forest appears to be relatively resistant to invasion by the exotic weed Darwin's barberry (*Berberis darwinii* Hook. Berberidaceae), probably because seedlings require relatively high light environments to establish successfully (McAlpine & Jesson 2008). It has been suggested anecdotally that New Zealand beech forest might be more susceptible to invasion by this weed species, since Darwin's barberry grows beneath both evergreen and deciduous *Nothofagus* in its native range (central to southern Chile and Argentina) (Ward 1965). Certainly, New Zealand beech forest is broadly similar both floristically and climatically to Chilean and Argentinean beech forest (Veblen et al. 1996), but it is uncertain whether this means that Darwin's barberry is able to establish equally well in similar forest in New Zealand.

Previous research has shown that first year survival of Darwin's barberry seedlings in New Zealand is low in podocarp-broadleaf forest where canopy openness is 10% or less (McAlpine 2005). In its native environment, Darwin's barberry seedlings appear to require a mean percentage canopy openness of at least 20.6% to survive (Figuroa & Lusk 2001). These results suggest that Darwin's barberry seedlings are unlikely to survive in New Zealand beech-broadleaf forest where the canopy remains intact. Conversely, adult plants are relatively shade tolerant and can survive being overtopped by other species (Allen 1991), so seedlings that establish in light gaps can grow to maturity and persist for many years. Adult plants appear to produce few flowers when growing in the shade (KGM pers. obs.), so such pockets of persistence do not necessarily become a source of further invasion.

Previous studies in New Zealand podocarp-broadleaf forest show that almost all viable Darwin's barberry seed germinates in the year following dispersal, and germinates regardless of environmental conditions, although most successfully in shadier sites (McAlpine & Drake 2003; McAlpine & Jesson 2008). This means that the spatial distribution of newly germinated seedlings in spring is reasonably indicative of the spatial distribution of dispersed seeds the previous summer. However, given that Darwin's barberry seedlings only survive under relatively high light conditions, distribution patterns of newly germinated seedlings tend to be incongruous with distribution patterns of older seedlings (McAlpine & Jesson 2008).

The aim of this project was to investigate survival of Darwin's barberry seedlings in mixed beech-broadleaf forest in New Zealand. Pure beech forest in New Zealand could also be vulnerable to invasion by Darwin's barberry, but we were unable to find any pure beech sites where Darwin's barberry occurred nearby. We asked the following questions:

1. Do Darwin's barberry seedlings survive beneath an intact beech-broadleaf canopy?
2. Does survival vary with canopy openness and/or distance from forest edge?
3. Are survival rates similar to those from podocarp-broadleaf forest?

2. Methods and materials

2.1 Study sites

In November 2006, we selected four study sites where Darwin's barberry occurs on the edge of mixed beech-broadleaf forest. This type of forest is likely to be broadly comparable with the mixed evergreen beech-broadleaf forest where Darwin's barberry occurs in its native range (Poole 1987; Veblen et al. 1996).

Two of the study sites were on either side of Whiskey Gully in the Blue Mountains at Tapanui (45°56'S, 169°15'E) in the South Island—one at the top of the east-facing slope, and the other at the top of the west-facing slope. The other two study sites were located within scenic reserves near Ohakune (39°24'S, 175°24'E) in the North Island: Rangataua Scenic Reserve and Mangaehuehu Scenic Reserve. Vegetation at all sites was largely composed of silver beech (*Nothofagus menziesii*) and black beech (*N. solandri*), with a range of broadleaf and podocarp species scattered throughout both the canopy and understorey. The two Tapanui sites also had red beech (*N. fusca*) present.

2.2 Experimental design

Five 50 m transects were laid out, a minimum of 3 m apart, at each of the four study sites. Transects started at a mature, fruiting Darwin's barberry plant on the edge of the beech forest and ran into the beech forest, perpendicular to the edge. Ten 0.25 m² plots were randomly allocated a position on each transect, one per 5 m section of the 50 m transect (10 plots × 5 transects × 4 sites = 200 plots).

Canopy cover was measured at each plot using a spherical crown densiometer (Lemmon 1957). This method was chosen so that results would be comparable to previous studies on Darwin's barberry where this methodology was used. Percent open sky to the north, south, east and west was measured, and these values were averaged. Readings were taken from 100–200 mm above each plot. In each plot, Darwin's barberry seedlings were counted at peak germination time in November 2006, and again 5 months later in April 2007. Seedlings were classified as either young (cotyledons present, soft green stem, likely to be <1 year old) or older (cotyledons gone, woody stem, likely to be >1 year old). Older seedlings were measured and individually marked so that survival rates could be calculated. Young seedlings were not marked, because they were too numerous and too fragile, so survival rates could only be estimated.

2.3 Statistical analyses

We tested whether distance from the forest edge affected canopy openness by fitting a linear mixed model using restricted maximum likelihood and specifying a Gaussian error distribution. The model included distance from edge as a fixed effect and transects nested within sites as random effects. We used model simplification by backward selection, comparing the effect of removing canopy openness from the maximal model on Akaike Information Criterion (AIC) values.

We used generalised linear mixed models (GLMMs) to analyse the abundance of young and older seedlings in both November and April, specifying a Poisson error distribution. We also used GLMMs to analyse survival of older seedlings from November to April. For this analysis, we specified a binomial error distribution with the number of seedlings in November, and the number of seedlings in November minus the number of seedlings in April as the binomial response variable. For each GLMM, we initially constructed a maximal model that included canopy openness and distance from forest edge as fixed effects, and transects nested within sites

as random effects. GLMMs were fitted using Laplacian approximation to maximum likelihood. We used model simplification by backward selection to construct final models, comparing the effect of removing each variable from the maximal model on AIC values. We proceeded with simplification of the model with the lowest AIC value until removing any variable increased the AIC value. The model with the lowest AIC value was selected as the final model. We ran all models using the lme4 package (Bates & Maechler 2009) in R version 2.9.2 (R Development Core Team 2009). There were a large number of plots with no Darwin's barberry seedlings, meaning the data contained large numbers of zeros. However, with binomial and Poisson error distributions the lmer command in the lme4 package automatically corrects for over-dispersion in the data if required.

3. Results

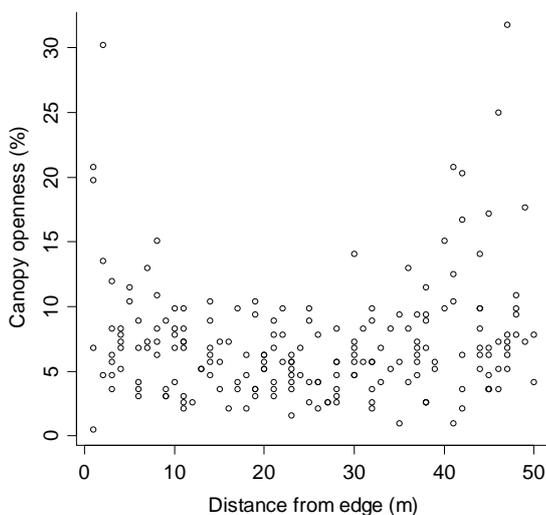
Mean canopy openness across all plots was 7.2% (\pm SD 4.6), and ranged from 0.5% to 31.8% (Fig. 1). Distance from the forest edge was not a significant predictor of canopy openness (Table 1).

Young seedlings

We counted a total of 491 young seedlings at peak germination time in November 2006, but by April 2007 only 112 were present. This represents an estimated survival rate of 23%. Distance from the forest edge was a significant predictor of the number of young seedlings present in both November and April (Table 1)—the abundance of young seedlings decreased with increasing distance from the forest edge (Table 2; Fig. 2). Canopy openness alone was not a good predictor of young seedling abundance, but models that included both distance and canopy openness had substantial support (Table 2). There was a weak, negative relationship between canopy openness and the abundance of young seedlings in November, and a weak positive relationship in April (Fig. 3).

Older seedlings

We counted a total of 61 older seedlings in November 2006, and 49 in April 2007—representing a survival rate of 80%. Of the 61 older seedlings, 49 were less than 5 cm tall, and the remaining 12 seedlings were classified into the approximate size classes as follows: 10 cm—three seedlings;



20 cm—two seedlings; 30 cm—one seedling; 40 cm—four seedlings; 50 cm—one seedling; 100 cm—one seedling. Both canopy openness and distance from forest edge were significant predictors of older seedling abundance in November and April (Table 1). Older seedling abundance decreased with increasing distance from the forest edge (Table 2; Fig. 2), and increased with increasing canopy openness (Fig. 3). Three models of survival of older seedlings from November to April had significant support:

1. Distance from forest edge,
2. Canopy openness,
3. Just the random effects (Table 1).

Figure 1. Distance from forest edge versus canopy openness across all four study sites. Each data point represents one plot ($n = 200$ plots).

Table 1. Generalised linear mixed models and linear mixed models fitted to data for canopy openness, the abundance of young and older seedlings, and older seedling survival. All models included transects nested within sites as random effects. Change in AIC was calculated as the difference in AIC between a model and the best-fitting (final) model, which has ΔAIC of 0. As a rule of thumb, models with $\Delta AIC \leq 2$ have substantial support**, those with $4 \leq \Delta AIC \leq 7$ weaker support*, and those with $\Delta AIC > 10$ virtually no support (Burnham & Anderson 2001).

| RESPONSE VARIABLE | EXPLANATORY VARIABLES | AIC | ΔAIC |
|-----------------------------------|----------------------------|--------|--------------|
| Canopy openness | Distance | 1186.0 | 6.0* |
| | None (random effects only) | 1180.0 | 0** |
| Young seedling abundance—November | Canopy openness + distance | 860.8 | 2.0** |
| | Canopy openness | 955.3 | 96.5 |
| | Distance | 858.8 | 0** |
| | None (random effects only) | 954.8 | 96.0 |
| Young seedling abundance—April | Canopy openness + distance | 346.4 | 0.6** |
| | Canopy openness | 395.0 | 49.2 |
| | Distance | 345.8 | 0** |
| | None (random effects only) | 393.0 | 47.2 |
| Older seedling abundance—November | Canopy openness + distance | 231.7 | 0** |
| | Canopy openness | 253.9 | 22.2 |
| | Distance | 241.6 | 9.9* |
| Older seedling abundance—April | Canopy openness + distance | 190.3 | 0** |
| | Canopy openness | 212.7 | 22.4 |
| | Distance | 200.6 | 10.3 |
| Older seedling survival | Canopy openness + distance | 40.7 | 2.8* |
| | Canopy openness | 39.4 | 1.6** |
| | Distance | 38.7 | 0.9** |
| | None (random effects only) | 37.8 | 0** |

Table 2. Final model parameter estimates and standard errors from GLMMs of the abundance of young and older seedlings and older seedling survival.

| RESPONSE VARIABLE | PARAMETER | ESTIMATE | SEM | z VALUE | P VALUE |
|-----------------------------------|-----------------|----------|--------|---------|---------|
| Young seedling abundance—November | Intercept | 0.7964 | 0.3373 | 2.361 | 0.0182 |
| | Distance | -0.0319 | 0.0033 | -9.581 | <0.0001 |
| Young seedling abundance—April | Intercept | -0.2209 | 0.3357 | -0.658 | 0.5110 |
| | Distance | -0.0496 | 0.0077 | -6.477 | <0.0001 |
| Older seedling abundance—November | Intercept | -1.1144 | 0.3259 | -3.419 | 0.0006 |
| | Canopy openness | 0.0751 | 0.0200 | 3.748 | 0.0002 |
| | Distance | -0.0437 | 0.0097 | -4.488 | <0.0001 |
| Older seedling abundance—April | Intercept | -1.3581 | 0.3614 | -3.757 | 0.0002 |
| | Canopy openness | 0.0842 | 0.0223 | 3.779 | 0.0002 |
| | Distance | -0.0494 | 0.0112 | -4.419 | <0.0001 |
| Older seedling survival | Intercept | 1.4685 | 0.3631 | 4.044 | <0.0001 |

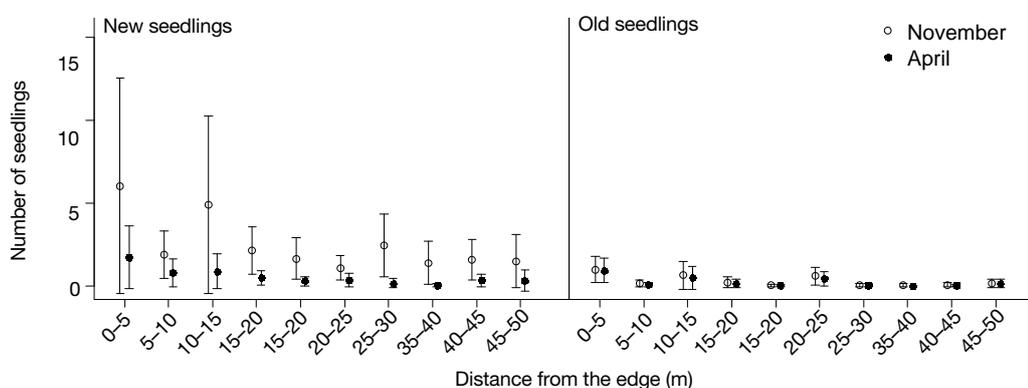


Figure 2. Abundance of young and older Darwin's barberry seedlings in November and 5 months later in April, as a function of distance from forest edge. Each data point represents the mean (\pm 95% CI) number of seedlings present in the 20 plots at each distance interval (one plot per distance interval for each of the 20 transects).

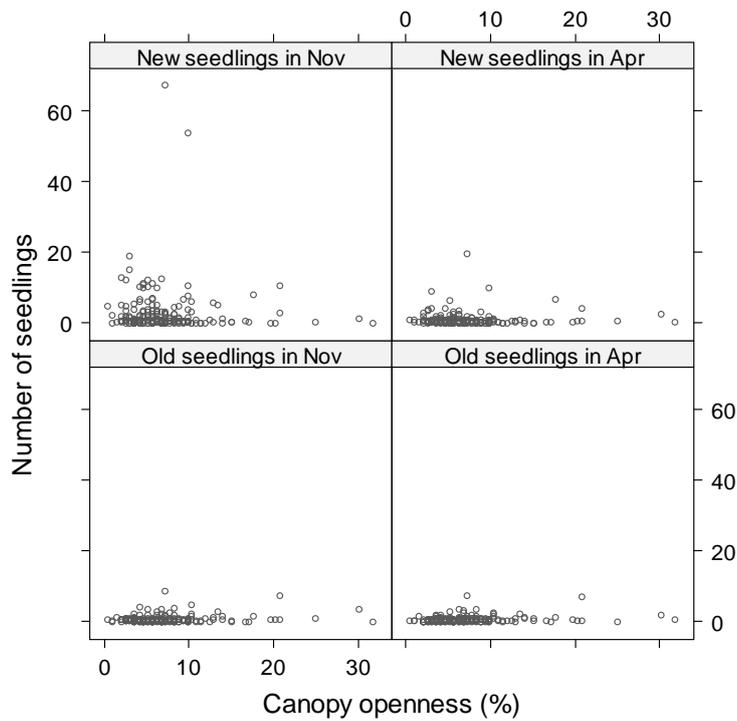


Figure 3. The relationship between canopy openness and the abundance of young and older Darwin's barberry seedlings in November and 5 months later in April. Each data point represents the number of seedlings present in one plot ($n = 200$ plots). Data points are jittered to allow overlaid points to be seen.

Table 3. Estimated 5-month-old Darwin's barberry seedling survival rates from previous studies beneath an intact podocarp-broadleaf forest canopy at the Karori Wildlife Sanctuary (Zealandia), Wellington (unpublished data, but see directed dispersal section in McAlpine (2005) for methods). Seedlings originated from seeds that had been naturally dispersed to 0.25 m² plots either directly beneath fuchsia (*Fuchsia excorticata*) trees or hinau (*Elaeocarpus dentatus*) trees, or to plots randomly placed elsewhere in the forest (non-hinau and non-fuchsia sites). Hinau and non-hinau sites were monitored for 2 consecutive years.

| TYPE OF SITE | NUMBER OF 0.25 m ² PLOTS | PERIOD MONITORED | INITIAL NUMBER OF SEEDLINGS | FINAL NUMBER OF SEEDLINGS | % SURVIVAL |
|--------------|-------------------------------------|--------------------------------|-----------------------------|---------------------------|------------|
| Hinau | 50 | September 2001 – February 2002 | 448 | 44 | 9.8 |
| Non-hinau | 50 | September 2001 – February 2002 | 394 | 22 | 5.6 |
| Fuchsia | 50 | October 2002 – March 2003 | 547 | 23 | 4.2 |
| Non-fuchsia | 50 | October 2002 – March 2003 | 253 | 10 | 4.0 |
| Hinau | 50 | October 2002 – March 2003 | 150 | 23 | 15.3 |
| Non-hinau | 50 | October 2002 – March 2003 | 138 | 1 | 0.7 |
| Average | | | 322 | 21 | 6.6 |

4. Discussion

Young seedlings were found at all distances along transects, indicating that seeds had been dispersed at least 50 m into the beech forest. Dispersal distances are likely to be considerably further, given that dispersed Darwin's barberry seeds have previously been detected 500 m from the source population (McAlpine & Jesson 2008), and birds are known to disperse seeds at least 1500 m in New Zealand (Wotton 2007). As expected, however, most young seedlings occurred near the forest edge, where the mature Darwin's barberry plants were located.

Canopy openness was not a strong predictor of the abundance of young seedlings, but results were in line with our expectations: young seedlings were more common in shadier sites (i.e. with lower canopy openness) in November, but were more common in sunnier sites (i.e. with higher canopy openness) 5 months later in April. This pattern is consistent with previous studies that show germination of Darwin's barberry seeds tends to be highest in shadier sites, but seedling survival tends to be highest in sunnier sites (McAlpine & Drake 2003; McAlpine & Jesson 2008). However, all sites in the current study were relatively shady (mean canopy openness 7.2%) and likely to be suitable for germination. An alternative explanation could be related to seed arrival patterns—some fruit-eating birds deposit seeds at highest densities beneath favoured perch trees (McDonnell & Stiles 1983), where canopy density may be higher. Conversely, seed densities are sometimes lowest in forest gaps, which have no suitable perches (Debussche & Isenmann 1994). The weak, positive relationship between canopy openness and the abundance of young seedlings in April is probably due to lower establishment success of Darwin's barberry seedlings in dense shade.

Previous studies of 5-month-old Darwin's barberry seedling establishment beneath intact podocarp-broadleaf forest show an average estimated seedling survival rate of 6.6% (unpubl. data; Table 3). This is considerably lower than the estimated survival rate of 23% from our study, suggesting that young seedlings may survive for longer in beech-broadleaf forest. However, given that our study was done in a different location and in a different year, we cannot rule out the possibility that other factors may have affected seedling establishment during the time period of our study. In any case, older seedlings are likely to be a more reliable indicator of establishment, since those seedlings had much higher survival rates over the course of our study, and had already survived for at least 1 year. Older seedlings were most abundant at higher-light sites close to the forest edge, which indicates that sites further into the forest tend to be less suitable for Darwin's barberry seedling establishment. These edge sites are also where most seeds are dispersed. Further, 5 months after germination, 80% of older seedlings that survived were less than 5 cm tall. We estimated that Darwin's barberry had been present at one of our sites for at least 35 years (estimated age of largest plant from annual rings), so if seedlings were able to establish beneath the intact canopy at these sites, we might expect to see many more older seedlings by now.

In summary, Darwin's barberry seedlings are unlikely to survive for long in New Zealand beech-broadleaf forest where the canopy remains intact. However, beech forest locally suffers from natural canopy collapse events (Wardle 1984), often resulting in discontinuous canopies with high light intensity gaps over large areas. It is likely that Darwin's barberry could exploit these events to invade further into beech forests, potentially spreading from forest gap to forest gap.

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