

## Biomass allocation, shade tolerance and seedling survival of the invasive species *Berberis darwinii* (Darwin's barberry)

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**Abstract:** *Berberis darwinii* (Berberidaceae) is a serious environmental weed in New Zealand, capable of invading a range of different light environments from grazed pasture to intact forest. According to optimal partitioning models, some plants optimise growth under different environmental conditions by shifting biomass allocation among tissue types (e.g. roots, shoots) to maximise the capture of limiting resources (e.g. water, light). We examined patterns of growth, biomass allocation, and seedling survival in *Berberis darwinii* to determine whether any of these factors might be contributing to invasion success. Growth and biomass allocation parameters were measured on seedlings grown for 7 months in five natural light environments in the field. Survival was high in the sunniest sites, and low in the shadiest sites. Seedlings grown in full sun were an order of magnitude taller and heavier, had five times as many leaves, and proportionally more biomass allocated to leaves than seedlings grown in other light environments. In the shade, leaves were bigger and thinner, and leaf area as a proportion of total plant biomass increased, but the proportion of above- to below-ground biomass was similar across all light and soil moisture environments. In summary, although leaf traits were plastic, patterns of biomass allocation did not vary according to optimal partitioning models, and were not correlated with patterns of seedling survival. Implications for the management of this invasive species are discussed.

**Keywords:** leaf traits; light; optimal partitioning models

## Introduction

Plasticity has long been considered a trait contributing to the success of weeds (Baker 1965; Roy 1990), but few empirical data exist to support or refute this assertion (Kolar & Lodge 2001). A species is said to be plastic if plants grown under different environmental conditions exhibit differences in morphological or physiological traits such as leaf characteristics (Popma et al. 1992; Ryser & Eek 2000), photosynthesis (Ellsworth & Reich 1992; Thompson et al. 1992), and overall patterns of biomass allocation (Grime et al. 1986; Chapin 1991; Wang et al. 1994). This occurs to some extent in most plants, but a more plastic species may be better able to optimise its capacity to acquire the most limiting resource and hence maximise growth in a wider range of habitats than a less plastic species (Latham 1992; Valladares et al. 2000). While there are, presumably,

costs associated with being plastic, this may be one way invasive species succeed over a wide range of environmental conditions and thus gain an advantage over native species (e.g. Williams et al. 1995; Fogarty & Facelli 1999; Stratton & Goldstein 2001).

One of the primary factors affecting seedling plasticity and growth is likely to be light availability (Kitajima 1996; Poorter 2001), although soil moisture (Williams et al. 1990; Veenendaal et al. 1996a), nutrient supply (Rincón & Huante 1994; Müller et al. 2000), herbivory (Schierenbeck et al. 1994), and competition (Grime 1979; Thébaud et al. 1996) can also be important. Light is an extremely heterogeneous resource (Chazdon et al. 1996), particularly in disturbed sites, which are often the point of entry for invasive species (Jesson et al. 2000; Lake & Leishman 2004), so it is an advantage for seedlings to be able to cope with a variety of light environments (Bazzaz 1996). Most species respond

– to some degree – to reduced irradiance by developing larger, thinner leaves and by increasing the ratio of total leaf area to total mass (Givnish 1988; Popma & Bongers 1988), but the link between root:shoot ratio and light environment is less consistent (Callaway 1992; Valladares et al. 2000), and may vary according to the shade tolerance of the species (Rao & Singh 1989). Optimal partitioning models suggest that plants can optimise growth in a variety of environments by shifting resource allocation to leaf and stem production in light-limited environments, and to root production in nutrient- or water-limited environments (Bloom et al. 1985; Tilman 1988). Many studies support these models (Mooney & Winner 1991; Canham et al. 1996; Poorter & Nagel 2000; Ryser & Eek 2000), although fewer have looked specifically at invasive species (but see Williams & Buxton 1989; Pattison et al. 1998; Longbrake & McCarthy 2001; Sanford et al. 2003).

In this study we examine the link between plasticity and invasiveness in the exotic species *Berberis darwinii* Hook. (Berberidaceae). *Berberis darwinii* is a woody, evergreen shrub up to 4 m high, native to southern Chile and Argentina. Initially brought to New Zealand as an attractive garden plant, it was first recorded naturalised 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). It has high reproductive capacity and efficient seed dispersal by birds in New Zealand, and can form dense colonies that persist after overtopping by forest trees (Allen 1991). It is tolerant of drought and frost, and can occupy a wide range of soil types (Allen 1991; Timmins & Mackenzie 1995). Plants can vary in growth habit, from dense shrubs with interlaced branches in open environments, to lianoid-like small trees up to 10 m tall beneath the intact forest canopy (Webb et al. 1988; Allen 1991). It is this variable growth form and observed tolerance of a range of environmental conditions that suggests a highly plastic species. We hypothesised that plasticity in leaf traits and biomass allocation according to light environment contributes to this ability to establish in a wide range of habitat types. To test this, we grew seedlings in a range of natural light environments in the field for 7 months. We then asked three questions: (1) do leaf traits and patterns of biomass allocation vary across light environments, (2) do patterns of seedling mortality also vary, and (3) is there any correlation between (1) and (2)?

## Methods

### Study site

We conducted this study within the Karori Wildlife Sanctuary, a 249-ha ecological restoration site in Wellington, New Zealand (41°18.3'S, 174°44.8'E).

Mean annual rainfall is 1235 mm, and mean annual temperature is 12.8°C (16.9°C in January and 8.8°C in July) (Greater Wellington Regional Council 2005; NIWA 2005). The predominant vegetation is regenerating native podocarp–broadleaved forest, with remnant pockets of planted *Pinus radiata* and other exotic species (Moles & Drake 1999). A large population of *Berberis darwinii* dominates the western hills adjacent to the sanctuary.

In order to establish the influence of different light environments on patterns of biomass allocation and seedling survival, we chose five types of sites within the sanctuary, based on differences in canopy openness: full sun, edge, understorey, sycamore, and deep shade. Full-sun sites were located near the centre of experimental treefall gaps. Some of these gaps were created in 1999 when groups of three to four *Pinus radiata* trees were felled for research purposes (McAlpine & Drake 2003), and others were created when large, single *Pinus radiata* trees were felled as part of the ecological restoration plan to eradicate exotic species from the sanctuary. Gaps were approximately 200 m<sup>2</sup> in size, and were surrounded by regenerating native forest. Edge sites were located within 5 m of the sunniest edge (approximately north-facing) of these treefall gaps. Understorey sites were located in areas of undisturbed canopy between gaps. Sycamore sites were located within mature stands of the exotic species *Acer pseudoplatanus* (sycamore). Sycamore is deciduous, so these sites are more seasonally variable than the evergreen sites in terms of the number of litter layers, soil moisture, and light levels. Deep-shade sites were located in the darkest accessible area of the sanctuary, beneath tall native forest, close to the shady side of a hill. Three replicates of each type of site were located, giving a total of 15 sites. Because the sycamore and deep-shade light environments were restricted to relatively small areas within the sanctuary, these sites may present a problem of pseudoreplication (Hurlbert 1984). Two of the sycamore sites were approximately 100 m apart, and the third was 500 m away. Similarly, two of the replicate deep-shade sites were within 50 m of each other, and the third was 400 m away. Accordingly, results are interpreted – and extrapolated – cautiously.

### Environmental measures

In order to establish the differences in environmental conditions associated with the range of light environments, we measured canopy openness, soil moisture, and number of litter layers at the microsites where seeds were sown (see below). To quantify percent canopy openness at each microsite we used hemispherical photography and Gap Light Analyser (GLA) software. We photographed the canopy directly above each microsite using a Sigma fisheye lens with a 180° field of view, scanned the photos and transformed

them into digital images, then analysed them with GLA software (Frazer et al. 1999). High mortality of seedlings in the sycamore and deep-shade light environments meant that seedlings were harvested from outside prepared microsites (see below), so hemispherical photographs were not directly attributable to particular seedlings. In these cases we averaged percent canopy openness over the three microsites in each site. Canopy cover in both sycamore and deep-shade sites was uniform, so variability among sites was likely to be minimal. In order to capture the spring–summer light environment that seedlings experienced for the duration of this experiment, we photographed the deciduous sycamore sites in January 2002. Timing was less important for the relatively stable canopy composition of the evergreen forest sites, so we photographed them in August 2001.

We measured soil moisture levels at each microsite on an overcast day in August 2001 using a Lincoln soil moisture meter. We inserted the moisture-sensitive probe 3 cm into the soil in each corner of each microsite, and took the average of these four values. Soil moisture is likely to vary throughout the year, but it is expected that the different sites are likely to vary in a similar way – except for the deciduous sycamore sites, which probably have deeper litter and thus higher soil moisture in winter compared with the other sites. To measure the number of litter layers, we counted the number of leaves pierced by a knife stabbed into the litter just outside each corner of each microsite, and averaged values for each light environment.

### Seedlings

*Berberis darwinii* seedlings were grown from seed in the 15 sites described above (three replicates each of five light environments: full sun, edge, understorey, sycamore, and deep shade). At each of the 15 sites, three replicate plots of approximately 1 m<sup>2</sup> were cleared of plants, litter, and other debris, then levelled, and covered with 1 cm of forest soil that had been heat-sterilised to kill any resident seeds. At each plot we sowed *Berberis darwinii* seeds that had been collected from within and around Karori Wildlife Sanctuary in February 2001, cleaned of fruit flesh and stored dry until required. Seeds were sown in March 2001. Within each plot, 100 seeds were sown onto a randomly allocated cell (20 × 20 cm), giving a total of 4500 seeds sown. A single layer of homogenised broadleaved litter, collected from within the sanctuary, was then placed on top of the seeds in an attempt to replicate the environmental conditions that naturally dispersed seeds would experience. A sheet of 1-cm mesh was placed directly on top of each plot to prevent birds from scratching in the loose litter and displacing seeds. Once the leaf litter had settled (July 2001) the mesh was removed. Most germination occurred in September 2001. Ten cells became overcrowded, so we thinned seedlings to allow

a minimum of 4 cm between any two plants. These 10 cells were excluded from survival analyses.

In March 2002 we harvested three randomly selected seedlings from each plot to measure growth and biomass allocation. Few seedlings had survived in the sycamore and deep-shade light environments so, where possible, we harvested naturally occurring, nearby seedlings that were obviously from the same cohort as the artificially sown seedlings (i.e. of a similar size and with the same lack of woody tissue). However, the total number of seedlings harvested did vary according to light environment: full sun, edge, and understorey: 45, sycamore: 44, and deep shade: 20. Following harvest, each seedling was cleaned, then divided into roots, stem, and leaves. Roots were sufficiently robust to withstand the harvest and cleaning process without damage, although fine hairs may have been lost. In March 2003 we counted the remaining seedlings, and calculated percentage survival. Seedlings that had been harvested were not included in survival analyses.

### Growth and biomass allocation measures

We measured total fresh leaf area with a Licor 320 leaf area meter. Spines (modified leaves) were present at the base of leaf clusters on the stems of well-developed seedlings that had grown in the full sun. These were often very similar in shape, form and colour to leaves, so we included them in the leaf analyses, along with healthy cotyledons. We also measured stem length and number of leaves while the seedlings were still fresh. We then dried the plant material at 45°C for 7 days before calculating total biomass, leaf area ratio (LAR, total fresh leaf area : total seedling mass), leaf mass ratio (LMR, total leaf mass : total seedling mass), and root : shoot ratio (root mass : stem + leaf mass). We weighed three dried leaves of known (fresh) area per seedling in order to calculate the average specific leaf area (SLA, leaf area per unit leaf mass) of each seedling.

### Statistical analyses

We analysed the data using S-Plus 4 (Mathsoft 1997) and SigmaStat 3.1 (SPSS 2004) statistical software. To identify the best way to transform the data, where necessary, we evaluated each variable for the best distribution of expected cf. actual residuals (Zar 1984). Number of litter layers, stem length, root mass, leaf mass, total biomass, total number of leaves, and total leaf area data were log-transformed. Proportion of root, stem, and leaf data were arcsin-transformed. All other data met model assumptions untransformed.

To examine differences in environmental measures (canopy openness, number of litter layers, and soil moisture) between light environments (full sun, edge, understorey, sycamore, and deep shade), we used one-way ANOVA with light environment as predictor and environmental measures as response variables,

followed by multiple pairwise comparisons. *P*-values of all post hoc pairwise multiple comparisons are Bonferroni-corrected (multiplied by the number of tests done). For all ANOVA analyses and pairwise multiple comparisons, results in which  $P < 0.05$  are reported as significant.

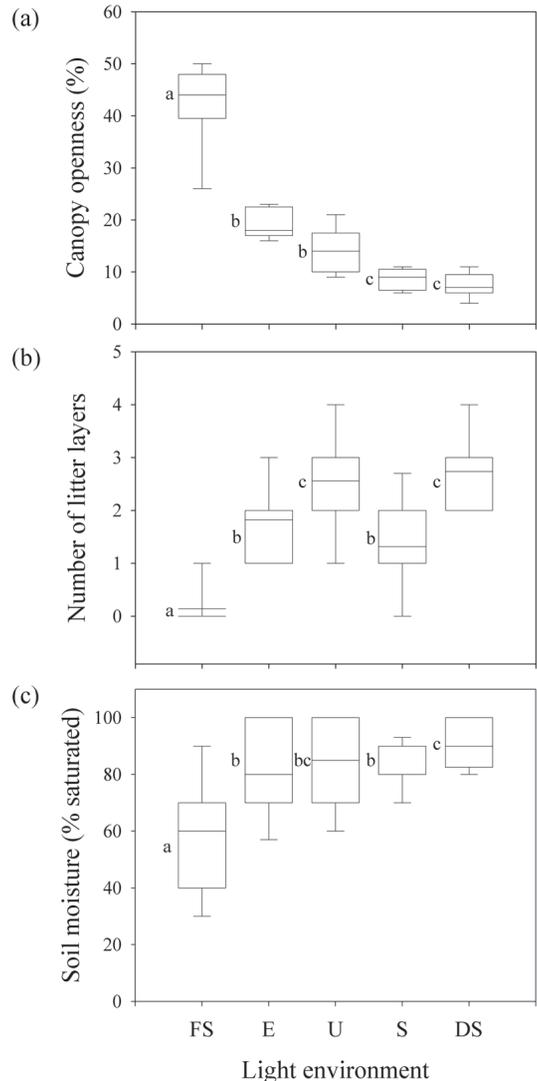
We used linear mixed-effects models to examine the effect of canopy openness, number of litter layers, soil moisture, and site (i.e. replicates of light environment) on percent seedling survival. We also used linear mixed-effects models to test for differences among light environment, site (nested within light environment), and plot (nested within site) of stem length, root mass, stem mass, leaf mass, total biomass, root:shoot ratio, number of leaves, total leaf area, LAR, LMR, and SLA, and Sidaks tests to make post hoc comparisons (site and plot are treated as random effects). Because allocation to roots, stem and leaves within a plant is not independent (i.e. values were measured on the same individuals and must sum to one), we used multivariate analysis of variance using the Wilks' lambda ( $\lambda$ ) ratio to test for differences among light environment, site (nested within light environment), and plot (nested within site) of proportion of biomass allocated to root, stem, and leaf.

## Results

There were significant differences among light environments for canopy openness (d.f. = 4,  $F = 74.05$ ,  $P < 0.001$ ), number of litter layers (d.f. = 4,  $F = 89.71$ ,  $P < 0.001$ ), and soil moisture (d.f. = 1,  $F = 8.30$ ,  $P < 0.001$ ) (Fig. 1). As expected, percent canopy openness was highest in the full sun, and lowest in the sycamore and deep-shade light environments, with intermediate values in the gap edges and understory (Fig. 1a). The number of litter layers was more variable, but was shallowest in the full sun (Fig. 1b). Soil moisture was significantly lower in the full sun, but was relatively similar in all other light environments (Fig. 1c).

Percent seedling survival was highest in the full sun ( $32.1 \pm 9.1$ ) and gap edges ( $19.5 \pm 7.7$ ) but only minimal in the understory ( $0.8 \pm 0.8$ ) (values reported in brackets are mean  $\pm$  1 SE). No seedlings survived in the two shadiest light environments (sycamore and deep shade). Seedling survival was significantly influenced by canopy openness (d.f. = 1,  $F = 25.37$ ,  $P < 0.001$ ), but not by soil moisture (d.f. = 1,  $F = 0.63$ ,  $P = 0.432$ ) or the number of litter layers (d.f. = 1,  $F = 1.79$ ,  $P = 0.190$ ). There was no effect of site (i.e. replication within light environment) (d.f. = 4,  $F = 1.28$ ,  $P = 0.297$ ).

All growth and biomass allocation parameters exhibited significant differences among light environments (Table 1). Seedlings grown in the full sun had at least 10 times more total biomass than seedlings



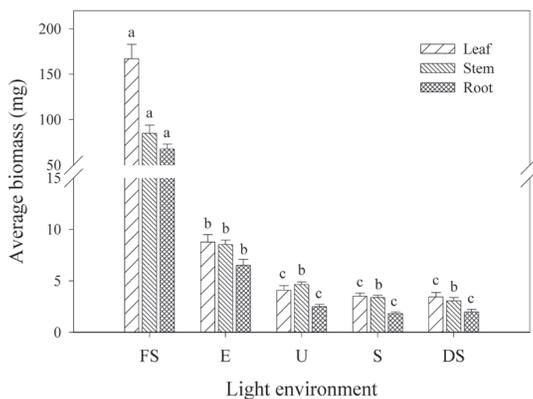
**Figure 1.** Box-plots of (a) canopy openness, (b) number of litter layers, and (c) soil moisture in different light environments (FS = full sun, E = edge, U = understorey, S = sycamore, DS = deep shade). The line within each box-plot indicates the median value, the lower and upper side of the box the 25<sup>th</sup> and 75<sup>th</sup> percentiles, and the error bars the 10<sup>th</sup> and 90<sup>th</sup> percentiles. Within each graph, boxes that share the same letter/s are not significantly different from each other ( $P < 0.05$ ). See Methods section for details on how each variable was measured.

grown in any other light environment (Fig. 2). Seedlings grown in the three shadiest light environments were small, with no significant difference in their average

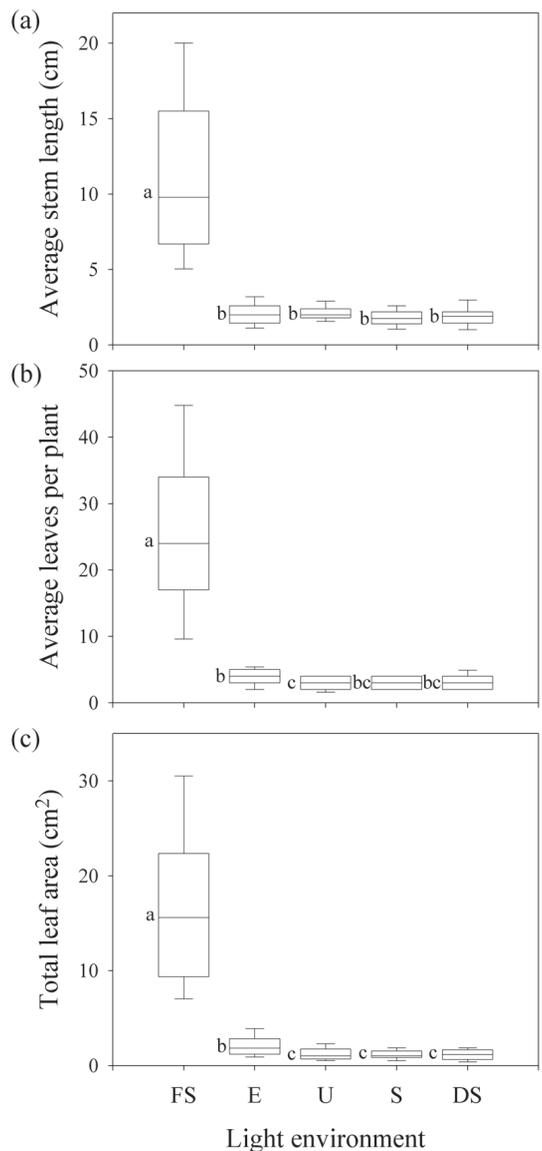
total biomass (Fig. 2). Seedlings from gap edges were significantly different from all others; smaller than the seedlings grown in full sun but larger than the seedlings grown in the understorey, sycamore, and deep shade light environments (Fig. 2). Seedlings grown in the full sun were also taller (Fig. 3a), with more leaves (Fig. 3b) and greater total leaf area (Fig. 3c) than seedlings grown in any other light environment.

**Table 1.** ANOVA using linear mixed-effects model of growth and biomass allocation parameters of *Berberis darwinii* seedlings by light environment, site (nested within light environment), and plot (nested within site). Site and plot were random effects, so only the results for the fixed effect (light environment) are presented. Summary table indicates variance ratios (*F*) and *P*-values. In all cases there are four degrees of freedom and 194 residual degrees of freedom.

Growth and biomass allocation parameters	<i>F</i>	<i>P</i>
Stem length	80.71	<0.001
Root mass	277.71	<0.001
Stem mass	323.66	<0.001
Leaf mass	273.50	<0.001
Total biomass	390.88	<0.001
Root:shoot ratio	5.05	<0.001
Number of leaves	203.04	<0.001
Total leaf area	174.18	<0.001
Leaf area ratio (LAR)	54.50	<0.001
Leaf mass ratio (LMR)	26.34	<0.001
Specific leaf area (SLA)	49.41	<0.001



**Figure 2.** Total leaf, stem, and root biomass of *Berberis darwinii* seedlings grown for 6 months in different light environments (FS = full sun, E = edge, U = understorey, S = sycamore, DS = deep shade). Within each tissue type, bars that share the same letter are not significantly different from each other ( $P < 0.05$ ). Error bars are  $\pm$  1 SE of the mean.



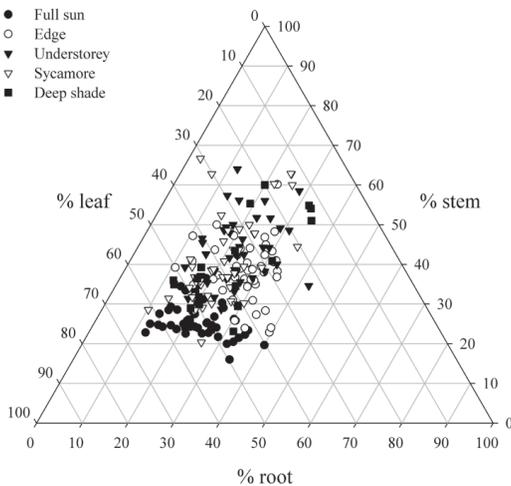
**Figure 3.** Box-plots of (a) stem length, (b) total number of leaves, and (c) total leaf area of *Berberis darwinii* seedlings grown for 6 months in different light environments (FS = full sun, E = edge, U = understorey, S = sycamore, DS = deep shade). The line within each box-plot indicates the median value, the lower and upper side of the box the 25<sup>th</sup> and 75<sup>th</sup> percentiles, and the error bars the 10<sup>th</sup> and 90<sup>th</sup> percentiles. Within each graph, boxes that share the same letter/s are not significantly different from each other ( $P < 0.05$ ).

According to the optimal partitioning model, we had expected plants growing in low light to allocate a higher proportion of biomass to shoots, and plants growing in high light to allocate a higher proportion to roots. However, contrary to our expectations, biomass allocation of *Berberis darwinii* did not vary in this way. Root:shoot ratios were similar in four of the five light environments (full sun  $0.31 \pm 0.02$ , understorey  $0.30 \pm 0.02$ , sycamore  $0.27 \pm 0.02$ , deep shade  $0.31 \pm 0.03$ ), with only the edge-site seedlings differing significantly ( $0.37 \pm 0.02$ ) (values are mean  $\pm$  SE). When biomass allocation was divided three ways

into root, stem, and leaf (rather than root and shoot), light environment did have a significant effect (Table 2). However, like most other parameters measured, it was only the seedlings grown in full sun that differed from the other light environments (Fig. 4). Post hoc comparisons indicated that seedlings grown in the full sun allocated more biomass to leaf and less to stem than seedlings from the other four light environments. Proportions of biomass allocated to roots, stem, and leaves in the edge, understorey, sycamore, and deep-shade light environments were similar.

**Table 2.** Multivariate analysis of variance of biomass proportions (root, stem, leaf) of *Berberis darwinii* seedlings by light environment, site (nested within light environment), and plot (nested within site). Summary table indicates degrees of freedom for Wilks lambda (d.f.), Wilks lambda (Wilks), the transformation of the Wilks lambda to an approximate *F* value (Approx *F*), numerator and denominator degrees of freedom, and *P*-values.

Biomass proportion	d.f.	Wilks	Approx <i>F</i>	num d.f.	den d.f.	<i>P</i>
Light environment	4	0.493	18.76	8	354	<0.001
Light environment:site	10	0.604	5.07	20	354	<0.001
Site:plot	6	0.940	0.94	12	354	0.514
Residuals	178					

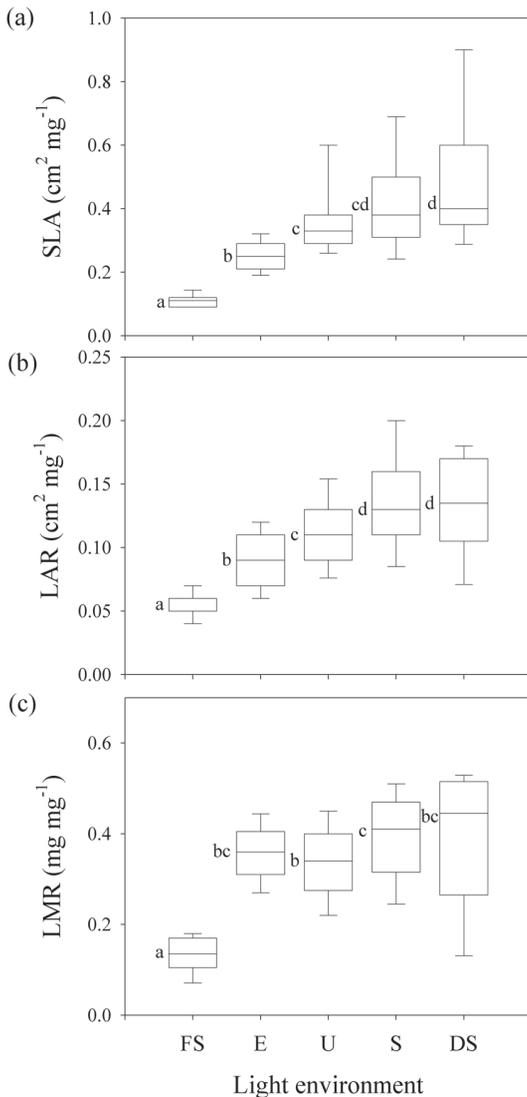


**Figure 4.** Proportion of biomass allocated to root, stem, and leaf in *Berberis darwinii* seedlings grown for 6 months in different light environments. Each data point is an individual seedling collected from that light environment ( $n = 45$  from full sun, edge, and understorey;  $n = 44$  from sycamore;  $n = 20$  from deep shade).

As expected, specific leaf area increased consistently as shade increased, with significant differences among four of the five light environments (Fig. 5a). Similarly, leaf area ratio increased consistently as canopy cover increased, although there was no significant difference among seedlings grown in the two shadiest light environments (Fig. 5b). Somewhat different was leaf mass as a proportion of total plant mass (leaf mass ratio). This was significantly lower in seedlings grown in the full sun, but was similar in all other light environments, with only seedlings from the understorey and sycamore light environments significantly different from each other (Fig. 5c).

## Discussion

Differential microhabitat recruitment can be an important factor influencing adult plant spatial patterns (Russell & Schupp 1998; Radford et al. 2002). In this study, seedlings survived well in the two sunniest sites, but died in the two shadiest sites. This gives a strong indication that *Berberis darwinii* seedlings are shade-intolerant. Interestingly, Allen (1991) surveyed existing *Berberis darwinii* seedlings in a range of light environments and concluded that establishment was enhanced by shade. However, this discrepancy between



**Figure 5.** Box-plots of (a) SLA (specific leaf area, leaf area per unit leaf mass), (b) LAR (leaf area ratio, total leaf area : seedling mass), and (c) LMR (leaf mass ratio, total leaf mass : seedling mass) of *Berberis darwinii* seedlings grown for 6 months in different light environments (FS = full sun, E = edge, U = understorey, S = sycamore, DS = deep shade). The line within each box-plot indicates the median value, the lower and upper side of the box the 25<sup>th</sup> and 75<sup>th</sup> percentiles, and the error bars the 10<sup>th</sup> and 90<sup>th</sup> percentiles. Within each graph, boxes that share the same letter/s are not significantly different from each other ( $P < 0.05$ ).

our two studies might be due to the different ways we considered 'shade'. Allen's estimation of percent cover was restricted to plants less than 2 m tall, so there may have still been significant light reaching the soil surface through such short-stature vegetation, depending on the density of canopy foliage. We measured percent canopy openness without regard to canopy height, but in most cases the canopy was approximately 5–8 m tall, so only the full sun and edge sites received any direct light. In other words, Allen's shady sites may in fact be comparable to our edge sites, and in both cases survival was high. Furthermore, Allen (1991) found that seedling densities were significantly higher in open and edge vegetation classes than beneath young and old forest, which is also consistent with our findings. However, it is likely that other environmental conditions varied between Allen's and our study.

While canopy openness was the strongest influence on seedling survival, this measurement alone may not account for all differences in light environment and hence seedling performance. Although edge and understorey sites were similar to each other in terms of canopy openness, the seedlings from these sites exhibited several significant differences: seedlings from edge sites had more leaves and lower specific leaf area than seedlings from understorey sites. This may be due to differences in the quality of light: the edges of forest gaps tend to receive more direct light than areas beneath the intact forest canopy, which tend to receive predominantly diffuse light (Chazdon & Fetcher 1984; Canham et al. 1990). Light beneath a canopy also has a different spectral composition and is strongly reduced in photosynthetically active radiation (Coombe 1957; Federer & Tanner 1966), and this too can affect seedling growth and survival (e.g. Schmitt & Wulff 1993; Tinoco-Ojanguren & Pearcy 1995). Likewise, the sycamore and deep-shade sites had similar levels of canopy openness, resulting in similar patterns of seedling growth and survival, but in the long term plants might perform differently in the two sites because the sycamore canopy is deciduous and therefore receives more light in winter. There are likely other factors beyond the scope of this study affecting seedling survival – for example, seedlings in the crowded full-sun sites might be further reduced by density-dependent mortality (Janzen 1970; Connell 1971; Harms et al. 2000). However, in general these results strongly suggest that the chances of a seedling surviving are highest within and around disturbed sites where light levels are relatively high.

High mortality of *Berberis darwinii* seedlings in the shade was unexpected, given that adult plants are shade-tolerant (Allen 1991; KGM pers. obs.). Other studies have shown shade-tolerant tree and shrub species to suffer high mortality in the shade as seedlings, possibly due to an increased presence of pathogens

(Augspurger & Kelly 1984; Weber et al. 2003) or herbivores (Baraza et al. 2004), or because young seedlings cannot fix enough carbon at low light levels to resist these stressors and persist in the understorey (Kobe 1997; Kaelke et al. 2001). For species like these, conditions required for establishment may be very different from conditions required for persistence. It is also possible that the shade-tolerance of *Berberis darwinii* increases as it ages, as has been suggested for other tree species (Kobe 1999; Weber et al. 2003). Other invasive species of *Berberis* show a similar pattern of seedling growth and survival: *B. thunbergii* tolerates a wide range of soil and light conditions and persists under dense canopies, but seedlings are rarely found in very shady conditions (Ehrenfeld 1999; Silander & Klepeis 1999), and growth and survival of *B. vulgaris* seedlings is poor under low light conditions (Kollmann & Reiner 1996). Light availability may be a limiting factor for the growth and survival of seedlings for all these species.

Seedlings grown in sunny sites also had significantly different growth patterns from seedlings grown in other sites. Sun-grown seedlings were an order of magnitude taller and heavier, and had five times as many leaves and a significantly higher leaf mass ratio than seedlings grown in other light environments. This general pattern is often characteristic of pioneer or light-demanding species (Bazzaz 1979; Veenendaal et al. 1996b) – as is low seedling survival in the shade (Denslow 1987; Kitajima 1994). Many species are able to regenerate in both high- and low-light environments (Welden et al. 1991), and can grow fast both in the sun and in the shade, relative to other species (Kitajima 1994; Poorter 1999), so are not easily classified into successional status. *Berberis darwinii* seems to be one such species, with traits of both early and late successional status: seedlings are largely restricted to high-light conditions, yet adults can persist in the shade.

Leaf mass ratio (LMR) of *Berberis darwinii* was low in the full-sun sites, and significantly higher in all four of the other, more shady, light environments. A similar study, which presented data for nine shrub and tree species growing in New Zealand, found that only about half of the species had a lower LMR in high light compared to low light, and the other half – which included two invasive species – had a similar LMR in both high- and low-light environments (Williams & Buxton 1989). This response appears to vary among species, and not necessarily in accordance with shade tolerance (Souza & Valio 2003). However, given that very few seedlings in this study survived in even moderate shade, there must be factors additional to LMR that affect *Berberis darwinii* survival in the shade. Further research might pinpoint causal factors. Other growth parameters also varied across light environments: specific leaf area (SLA) and leaf area ratio

(LAR) increased as light levels decreased. However, most plants increase SLA and LAR in response to low light levels (Boardman 1977; Givnish 1988), so these traits on their own are unlikely to be major factors contributing to invasion success.

While there was some variation in biomass allocation across sites, this too was largely due to the fact that seedlings grown in full-sun sites were so different from seedlings grown in the other four light environments, and allocated considerably more carbon to leaves. In general, proportional allocation to above- and below-ground biomass did not vary according to the optimal partitioning hypothesis, despite significant differences in the light and soil moisture environment. Several studies have found similar results for invasive species (Pattison et al. 1998; Schweitzer & Larson 1999), but others have not (Williams & Buxton 1989; Baruch et al. 2000). Similarly, non-invasive species may or may not exhibit morphological plasticity in biomass allocation when grown along a light gradient (Lusk & Del Pozo 2002; Montgomery 2004). It appears this trait is species-specific, and not necessarily linked to invasiveness per se. Furthermore, many phenotypic traits change during the life of a plant (Poorter & Pothmann 1992; Coleman et al. 1994; Gedroc et al. 1996), so patterns of biomass allocation may be different – including more plastic – later in life.

In summary, the success of *Berberis darwinii* in a wide range of environments does not appear to be explained by plasticity in proportional biomass allocation at the seedling stage. Some leaf traits did vary consistently across light environment, but this is likely to be the case for native species too. First-year seedling survival was low in the shade, despite adult plants of *Berberis darwinii* commonly occurring beneath an intact forest canopy. These results have implications for the management and control of this invasive species, where it occurs in similar conditions. While adult plants may be found in almost any light environment, the main focus of seedling control should be in and around high-light areas such as canopy gaps and other disturbed areas, since the majority of first-year seedlings growing beneath the closed canopy will likely die off naturally.

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