

Photosynthesis and water-use efficiency: A comparison between invasive (exotic) and non-invasive (native) species

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Abstract Invasive species have been hypothesized to out-compete natives through either a Jack-of-all-trades strategy, where they are able to utilize resources effectively in unfavourable environments, a master-of-some, where resource utilization is greater than its competitors in favourable environments, or a combination of the two (Jack-and-master). We examined the invasive strategy of *Berberis darwinii* in New Zealand compared with four co-occurring native species by examining germination, seedling survival, photosynthetic characteristics and water-use efficiency of adult plants, in sun and shade environments. *Berberis darwinii* seeds germinated more in shady sites than the other natives, but survival was low. In contrast, while germination of *B. darwinii* was the same as the native species in sunny sites, seedling survival after 18 months was nearly twice that of the all native species. The maximum photosynthetic rate of *B. darwinii* was nearly double that of all native species in the sun, but was similar among all species in the shade. Other photosynthetic traits (quantum yield and stomatal conductance) did not generally differ between *B. darwinii* and the native species, regardless of light environment. *Berberis darwinii* had more positive values of $\delta^{13}\text{C}$ than the four native species, suggesting that it gains more carbon per unit water transpired than the competing native species. These results suggest that the invasion success of *B. darwinii* may be partially explained by combination of a Jack-of-all-trades scenario of widespread germination with a master-of-some scenario through its ability to photosynthesize at higher rates in the sun and, hence, gain a rapid height and biomass advantage over native species in favourable environments.

Key words: *Berberis darwinii*, invasive, native, New Zealand, photosynthesis, water-use efficiency.

INTRODUCTION

Invasive plant species can drastically alter ecosystem-level processes by changing community structure and dynamics, soil water and nutrient levels, substrate stability, rates and pathways of succession, and disturbance and fire regimes (Vitousek & Walker 1989; Hughes *et al.* 1991; D'Antonio & Vitousek 1992; Walker 1993; Cronk & Fuller 1995; Ehrenfeld *et al.* 2001). How and why this happens is a question that has long interested population ecologists (Mack 1985; Vitousek 1990), but is also of practical interest to managers dealing with invasive species (Allendorf & Lundquist 2003; Donlan *et al.* 2003). Successful invasive species can have life history and morphological traits that enable them to out-compete native species, such as more prolific seed production and dispersal, longer flowering periods, higher rates of seedling recruitment, more efficient leaf arrangement, faster growth rates, better recovery from leaf loss, or greater

phenotypic plasticity (Williams *et al.* 1995; Ehrenfeld 1999; Fogarty & Facelli 1999; Lavergne *et al.* 1999; Martin 1999; Durand & Goldstein 2001a).

Recently, it has been proposed that invasive species may out-compete natives through a Jack-of-all-trades scenario, where the invader is able to maintain fitness in unfavourable environments, a master-of-some scenario, where invasives are better able to increase fitness in favourable environments, or some combination of the two (Richards *et al.* 2006). Richards *et al.* (2006) suggest that Baker's (1965) ideal weed would display a combination of these two strategies (Jack-and-master) by maintaining fitness in resource-poor environments, and maximizing fitness in favourable conditions (Fig. 1). Because physiological traits involved in resource acquisition contribute directly to fitness, this framework provides testable predictions about the responses of physiological traits of an invader to favourable and unfavourable environments. For example, under a Jack-of-all-trades scenario, resource acquisition will be high in both environments and so an invader would show little variation in physiological traits (Fig. 1a), whereas a

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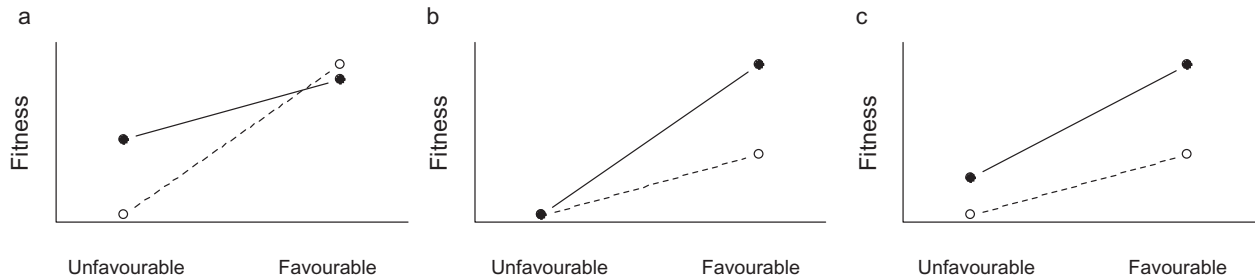


Fig. 1. Predicted fitness responses of an invader (solid line) and a non-invader (dashed line) to an unfavourable and a favourable environment for (a) a Jack-of-all-trades strategy, (b) a master-of-some strategy and (c) a Jack-and-master strategy. If the invader has a Jack-of-all trades or master-of-some strategy this will result in a significant interaction between environment and invasiveness, and there will be a significant effect of invasiveness (and often a significant interaction) for a Jack-and-master strategy. Redrawn from Richards *et al.* (2006).

master-of-some invader would only exhibit increased resource acquisition in the favourable environment, and thus would demonstrate greater variation in physiological traits across environments. Here we use a multi-species comparison of resource-acquisition traits in an invader and four co-occurring native species to test the hypothesis that an invader will have greater resource acquisition across environments compared with co-occurring species, and in addition, will respond considerably more to favourable environments (i.e. Jack-and-master).

In this study we focused on physiological traits related to carbon gain, as these traits will directly influence a plant's fitness, and thus differences between invasive and native species across environments likely reflect an invader's strategy of competition. Moreover, physiological attributes such as higher rates of photosynthesis have been shown to confer an advantage to exotic species over natives, and hence contribute to invasion success. For example, Kloeppel and Abrams (1995) found that the invasive tree species *Acer platanoides* had greater carbon assimilation (i.e. higher net photosynthesis) than the native *A. saccharum*. Pattison *et al.* (1998) compared five invasive species with four native Hawaiian species, and found that all invasive species had higher rates of net photosynthesis than the natives. But how might a higher rate of photosynthesis contribute to invasion success? Plants with high photosynthetic capacity generally exhibit high rates of biomass accumulation and growth (Lambers & Poorter 1992), and therefore may be able to out-compete slower-growing species and rapidly colonize a large area (Grime & Hunt 1975). Specific leaf area (SLA, leaf area per unit leaf mass) is also a key component of a species' growth strategy, because it describes the light-capture area deployed per unit leaf mass (Lambers & Poorter 1992). So, if invasive species have higher maximum rates of photosynthesis and higher SLA than native species, they may be

better able to capture and utilize light resources – particularly in high-light environments associated with disturbance that are often the entry point for invasive species (Hobbs 1989; Petryna *et al.* 2002).

Greater water-use efficiency (WUE) is another trait that has the potential to contribute to invasion success. Water-use efficiency is the amount of carbon gained per unit water transpired (Farquhar *et al.* 1989). Carbon gain is often increased by stomatal opening, but this in turn results in greater water loss via transpiration. Thus, efficient water use requires that stomatal opening is optimized for the conflicting problems of reducing water loss and increasing CO₂ uptake (Cowan 1982). Water-use efficiency can also be enhanced by increasing biomass allocation to root tissue, or by storing water for later use (Gordon *et al.* 1999; Li 1999).

Here we use a multiple-species comparison of invasive Darwin's barberry (*Berberis darwinii* Hook. Berberidaceae) and four co-occurring ecologically similar native New Zealand species: *Coprosma grandifolia* (Rubiaceae), *Meliccytus ramiflorus* (Violaceae), *Pseudopanax arboreus* (Araliaceae) and *Schefflera digitata* (Araliaceae). We hypothesized that a higher rate of photosynthesis and more efficient use of water in both stressful and non-stressful environments might give *B. darwinii* an advantage over native species, and thus contribute to invasion success. *Berberis darwinii* is a woody, evergreen shrub up to approximately 4 m high, native to southern Chile and Argentina. It was originally brought to New Zealand for horticultural purposes, but has since invaded many vegetation types throughout the country (Webb *et al.* 1988). It forms dense, impenetrable stands that exclude native species, and can also persist beneath the native forest canopy (Allen 1991). The co-occurring native species are all small trees *c.* 7–10 m tall, common in both sunny and shady conditions in lowland and montane forest throughout much of New Zealand (Allan 1961; Poole & Adams 1994).

METHODS

Study site

We conducted this study 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 1235 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* and other exotic species.

Seed sowing experiments

To examine germination and seedling establishment, we sowed seeds at three light environments based on differences in canopy openness: full sun (near the centre of a treefall gap), understory (in areas of undisturbed canopy between gaps) and deep shade (located in the darkest accessible area of the KWS, beneath tall native forest, close to the side of a hill). Three replicates of each type of site were located, giving a total of nine sites.

At each of the nine sites, we cleared three 1-m² replicate plots of plants, leaf litter and other debris, then covered each one with 1 cm of forest soil that had been heat-sterilized to kill any resident seeds. At each plot we sowed fresh seed of the five study species, which we had collected from within and around the KWS between February and April 2001. Seeds were sown in March 2001, except for seeds of *Schefflera*, which fruits later than the other species and so were sown in May. Within each plot, we sowed 100 seeds of each species (although only 50 of the larger-seeded *Coprosma* were sown per cell) onto a randomly allocated, 200 mm × 200 mm cell. An empty cell (also 200 mm × 200 mm) was left between each species to facilitate seedling identification. In an attempt to replicate the environmental conditions that naturally dispersed seeds experience, we placed a single layer of homogenized broadleaf litter on top of the seeds. We then placed a sheet of metal mesh with 1-cm² apertures directly on top of each plot to prevent birds from scratching and displacing seeds. This mesh was removed in July 2001 to avoid damage to the seedlings. Ten cells became overcrowded, so were excluded from survival analyses.

We counted seedlings in November 2001 to estimate per cent germination. To account for naturally dispersed seeds, we adjusted germination data according to the number of seedlings that appeared in the nine

cells outside each species' designated subplot: $G_f = G_d - G_o/9$; where G_f = final germination, G_d = number of germinated seeds in species' designated cell, G_o = total seeds germinated in nine other cells. These adjustments had little impact on final germination percentages. We re-counted seedlings in March 2003 to calculate per cent survival. These methods and survival data for *B. darwinii* are also reported elsewhere in relation to patterns of biomass allocation (McAlpine & Jesson, 2007).

Photosynthesis

We measured photosynthesis within and around the KWS between January and April 2003 using a portable open gas-exchange system (LI-6400, Licor, Lincoln, NE, USA) with a blue-red LED light source (6400-02B, Licor). We selected 10 plants per species, a minimum of 50 cm and up to 4 m tall: 5 growing in full sun and 5 growing in shade beneath the native forest canopy. We chose one recently matured, fully expanded leaf per plant for the measurements, giving a total of 10 leaves measured per species. Leaf temperature was kept at approximately 19°C during all measurements, similar to daytime summer temperatures in the shade. Sample CO₂ concentration was 370 μmol mol⁻¹, and leaf-to-air vapour pressure deficit was held between 1.0 and 1.5 kPa. The order of measurements of each species was varied on a day to reduce biases due to the effects of changes in plant temperature on photosynthetic rates. To compare the steady-state photosynthetic performance in sun and shade of each species, a light-response curve was generated for each leaf using the automated routine in the LI-6400. Prior to measurements, leaves were allowed to acclimate under a photosynthetic photon flux density (PPFD) of either 1500 μmol m⁻² s⁻¹ (for plants grown in sun) or 1000 μmol m⁻² s⁻¹ (for plants grown in shade). Once stable, leaves were exposed to a series of PPFDs decreasing from that initial level to darkness: 1500, 1000, 500, 200, 100, 50, 10 and 0 μmol m⁻² s⁻¹. At each light level, we allowed the photosynthetic rate to stabilize for 2–4 min before recording photosynthetic rate. Upon completion of the light-response curve, we harvested the measured leaf for determination of SLA (leaf area/leaf mass). Leaf area was measured using a Licor 3100 area meter; samples were then dried for 7 days at 45°C, and weighed.

We quantified the degree of canopy cover at each plant using a crown densiometer (Forestry Suppliers, USA) to estimate canopy openness. This instrument is composed of 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).

Water-use efficiency

We measured the carbon isotope composition ($\delta^{13}\text{C}$) of leaves to compare photosynthetic WUE of the five study species in sunny and shady environments (for theory and methods, see Craig 1957; Farquhar & Richards 1984; Farquhar *et al.* 1989). Leaves were collected from the same areas where the photosynthetic measurements were made, although they were not collected from the same plants. We harvested one recently expanded leaf per plant in June 2006. This gave a total of 10 leaves per species measured – 5 per light treatment. Each leaf was air-dried at 45°C for 7 days, then finely ground (<3 mm) using a mortar and pestle. Samples were then sent to the Stable Isotope Unit at the University of New Brunswick, Canada, for analysis of $\delta^{13}\text{C}$ ratios (<http://www.unb.ca/cri/sinlab/>).

Statistical analyses

The response of photosynthesis to PPFD is described by a non-rectangular hyperbola (Ögren & Evans 1993). Curve fitting was conducted in SigmaPlot, using the following equation:

$$A = \frac{\alpha I + A_{\max} - \sqrt{(\alpha I + A_{\max})^2 - 4\theta\alpha I A_{\max}}}{2\theta} - r_d$$

where A is the net carbon assimilation rate, α is quantum yield (the initial slope of the light-response curve), I is incident PPFD, A_{\max} is the light-saturated photosynthetic capacity, r_d is dark respiration, and θ is a curvature parameter (see Ögren 1993). We multiplied light-saturated photosynthetic rate by SLA to obtain an estimate of photosynthetic rate on a per-unit-mass basis.

We analysed the data using R (R Development Core Team 2006). To specifically test the hypothesis that invasive *B. darwinii* responds differently to stressful and favourable conditions compared with the other native species (see Fig. 1), we tested for the interaction between invasiveness (*B. darwinii* vs. all other native species) and canopy openness on germination, survival, and photosynthetic and leaf characteristics of the wild plants growing in sun and shade. We also examined the effect of species (nested within invasiveness category) and all two-way interactions. To identify the best way to transform the data, we evaluated each variable for the best distribution of expected versus actual residuals (Zar 1984). Mass-based estimates of maximum photosynthesis rate, and dark respiration were log-transformed, quantum yield was square root transformed, but all other data met model assumptions untransformed. For measures of WUE, we did not make measures of canopy cover above the plants from which leaves were collected, so light environment was analysed as a categorical predictor (shade and sun).

RESULTS

Germination and survival of seeds sown in the field

Berberis germinated more successfully across the range of light environments than any of the native species (Fig. 2a). *Pseudopanax*, *Melicytus* and *Coprosma* all have transient seed banks, but *Schefflera* has persistent seeds, so germination rates may be underestimated for this species (Moles *et al.* 2000). Per cent germination was significantly affected by per cent canopy openness for all species (Table 1), but the response of invasive

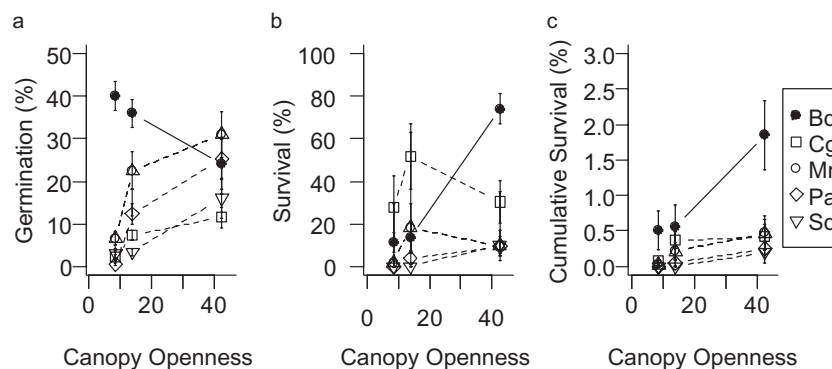


Fig. 2. (a) Germination; (b) survival of germinated seeds after 18 months; and (c) cumulative germination and survival of seeds sown of *Berberis darwinii* (solid line) and four co-occurring native species (dashed lines) sown in contrasting light environments. Each value represents the mean parameter value (± 1 standard error) at the average canopy openness for each light environment. Species are: Bd, *Berberis darwinii*; Cg, *Coprosma grandifolia*; Mr, *Melicytus ramiflorus*; Pa, *Pseudopanax arboreus*; Sd, *Schefflera digitata*.

Table 1. Generalized linear models of per cent germination, per cent survival of germinated seedlings after 18 months and cumulative survival of all seeds sown after 18 months for invasive *Berberis darwinii*, and co-occurring native species *Coprosma grandifolia*, *Melicytus ramiflorus*, *Pseudopanax arboreus* and *Schefflera digitata* by canopy openness, invasive strategy (*B. darwinii* vs. all other species), species nested within invasive strategy, and their two-way interactions

Parameters	d.f.	dev	F	P
Germination				
Per cent canopy openness	1	63.09	32.06	<0.001
Invasiveness	1	159.78	81.17	<0.001
Species (invasiveness)	3	60.00	10.16	<0.001
Canopy openness × invasiveness	1	64.75	32.89	<0.001
Canopy openness × species (invasiveness)	3	11.85	2.00	<0.001
Residual	125	246.05		
Survival				
Per cent canopy openness	1	28.47	13.22	<0.001
Invasiveness	1	46.58	21.62	<0.001
Species (invasiveness)	3	54.25	8.40	<0.001
Canopy openness × invasiveness	1	12.50	5.80	0.017
Canopy openness × species (invasiveness)	3	5.32	0.83	0.48
Residual	125	269.28		
Cumulative germination and survival				
Per cent canopy openness	1	63.09	32.05	<0.001
Invasiveness	1	159.78	81.17	<0.001
Species (invasiveness)	3	60.00	10.16	<0.001
Canopy openness × invasiveness	1	64.75	32.89	<0.001
Canopy openness × species (invasiveness)	3	11.85	2.00	0.12
Residual	125			

Summary table indicates degrees of freedom (d.f.), deviance (dev), variance ratios (F) and P-values (P).

Berberis significantly differed from the native species, resulting in a significant interaction between canopy openness and invasiveness: germination of *Berberis* was highest in shadier sites, while germination of native species was highest in sunnier sites (Fig. 2a). The native species also differed in their germination responses to the different light environments, resulting in a significant effect of species nested within invasive category and an interaction between species and canopy openness.

Seedling survival of all species was significantly influenced by canopy openness (Table 1). Twelve months after germination, there were no seedlings of *Pseudopanax* or *Schefflera* alive in the shadiest site and only a few *Berberis* seedlings in the deep shade and understorey sites (Fig. 2). There was a significant interaction between canopy openness and invasive strategy, suggesting that *B. darwinii* responded to contrasting light environments differently compared with the native species. While seedling survival of *B. darwinii* was lower than two native species in the shaded sites, survival was over twice that of all native species in the high-light environment. There was also a significant effect of species nested within invasive strategy, suggesting that the native species had significantly different survival across light environments.

Cumulatively, the total proportion of seeds sown of *B. darwinii* that germinated and then survived as seedlings for 18 months was significantly higher compared

with all other species across light environments (Fig. 2c, Table 1). General linear models revealed a significant effect of invasiveness and canopy openness on cumulative germination and survival, and a significant interaction between the two, suggesting that germination and survival of *B. darwinii* differed from the native species across light environments. There was also a significant effect of species nested within light environment, and a significant interaction between species and light environment.

Photosynthetic and water-use parameters

Light-response curves differed between light environments in the same way for all species, in that leaves developed in shade had significantly lower light-saturated photosynthesis rates, and they saturated at lower PPFDs than sun leaves (Fig. 3). However, in the sunny sites *B. darwinii* had a higher rate of light-saturated photosynthesis than the native species, and light saturation occurred at higher PPFDs. Light-response curves in the shade were similar for all species (Fig. 3).

The average area-based estimate of light-saturated photosynthetic rate (A_{\max}) differed by both canopy openness and invasiveness, and there was a significant interaction between the two parameters (Table 2). *Berberis darwinii* had significantly higher light-saturated

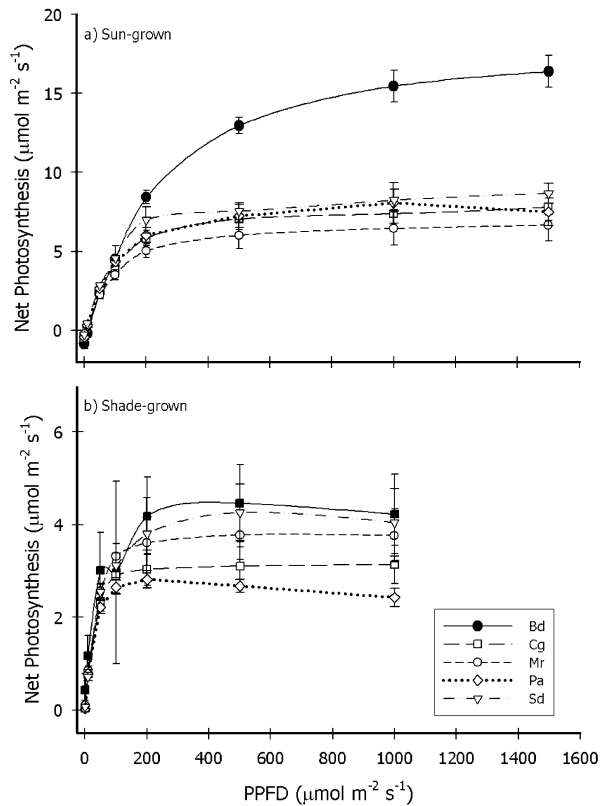


Fig. 3. Light-response curves from wild plants *Berberis darwinii* (solid line) and four co-occurring native species (dashed lines) growing in (a) sun and (b) shade. Each point represents the average photosynthetic rate of five leaves in the given light environment. Curves are non-rectangular hyperbolae (see *Methods* section for equation) fitted through mean values of photosynthesis recorded at each photosynthetic photon flux density (PPFD). Species are: Bd, *Berberis darwinii*; Cg, *Coprosma grandifolia*; Mr, *Meliclytus ramiflorus*; Pa, *Pseudopanax arboreus*; Sd, *Schefflera digitata*.

photosynthetic rates than the native species in full sun, but not in more closed-canopy environments (Fig. 4a). However, when light-saturated photosynthetic rate was expressed on a per-mass basis, there was a significant effect of species nested within invasive category, but no significant effect of any other parameter (Table 2, Fig. 4b).

Berberis darwinii had similar respiration rates as the native species in the shaded environments, but had considerably higher rates in sunnier sites (Fig. 4c). This resulted in a significant interaction between invasiveness and canopy openness (Table 2). Respiration rates increased with canopy openness in all species. There was no effect of invasive strategy or species (nested within invasive strategy).

The interaction between invasiveness and canopy openness was not significant for any of the other parameters derived from the light-response curves. While quantum yield was significantly higher in

closed-canopy environments, there was no difference in quantum yield between *B. darwinii* and the other four native species (Table 2), or a significant interaction between canopy openness and invasive strategy. *Berberis darwinii* had higher stomatal conductance than all species except *S. digitata*. Stomatal conductance varied among species and light environments, resulting in a significant interaction of species (nested in invasive strategy) and light environment (Table 2, Fig. 4d).

Specific leaf area varied significantly between *B. darwinii* and the other native species and across light environments, but there was no significant interaction between the two (Table 1). While SLA was higher (leaves were larger and thinner) in the shade for all species (Fig. 4e), it was lower for *B. darwinii* and *S. digitata* than for all other species.

Mean $\delta^{13}\text{C}$ values ranged from -33.0‰ to -26.2‰ (Fig. 4f). There was a significant effect of canopy openness and a significant difference between *B. darwinii* and the native species for $\delta^{13}\text{C}$, but no interaction between the two (Table 2). Within species, $\delta^{13}\text{C}$ values declined as canopy openness increased, indicating a decline in WUE.

DISCUSSION

The success of an invader may be due either to its ability to maintain fitness in unfavourable conditions (a Jack-of-all-trades invasion strategy), a greater ability to increase fitness when conditions are favourable (master-of-some), or to a combination of the two (Richards *et al.* 2006). Physiological traits should respond to stressful or favourable environments according to the strategy of the invader. Here we found that invasive Darwin's barberry (*B. darwinii*) in New Zealand exhibited a combination of strategies: germination was less variable than other species across environments (i.e. Jack-of-all-trades), while seedling survivorship and area-based estimates of light-saturated photosynthetic rates were approximately double that of all four co-occurring native species studied in sunny environments, but similar in shady environments, suggesting a master-of-some strategy. We suggest it is this combination of strategies in different life-history traits that contributes to the invasiveness of this species.

While many studies have found evidence that some invasive plants photosynthesize at higher rates than natives generally (Carter *et al.* 1989; Owens 1996; Pattison *et al.* 1998; Baruch *et al.* 2000; Durand & Goldstein 2001b; McDowell 2002), higher photosynthetic rates in a single environment may be sufficient to contribute to invasion success, as higher carbon gain likely increases fitness in that environment. Plants with higher photosynthetic capacity do not always exhibit

Table 2. Generalized linear model of photosynthetic and leaf parameters for invasive *Berberis darwinii*, and co-occurring native species *Coprosma grandifolia*, *Melicytus ramiflorus*, *Pseudopanax arboreus* and *Schefflera digitata* by canopy openness, invasive strategy (*B. darwinii* vs. all other species), species nested within invasive strategy, and their two-way interactions

Photosynthetic and leaf parameters	d.f.	dev	F	P
A_{max} (area based)				
Per cent canopy openness	1	597.31	86.24	<0.001
Invasiveness	1	198.01	28.58	<0.001
Species (invasiveness)	3	44.02	2.12	0.11
Canopy openness × invasiveness	1	98.92	14.28	<0.001
Canopy openness × species (invasiveness)	3	16.73	0.81	0.49
Residual	40	16.73		
A_{max} (mass based)				
Per cent canopy openness	1	0.078	0.85	0.37
Invasiveness	1	0.0062	0.067	0.80
Species (invasiveness)	3	4.14	15.08	<0.001
Canopy openness × invasiveness	1	0.04	0.40	0.53
Canopy openness × species (invasiveness)	3	0.71	2.61	0.06
Residual	40	3.66		
Dark respiration				
Per cent canopy openness	1	1.54	54.71	<0.001
Invasiveness	1	0.08	2.77	0.10
Species (invasiveness)	3	0.03	0.32	0.81
Canopy openness × invasiveness	1	0.18	4.18	0.047
Canopy openness × species (invasiveness)	3	0.02	0.26	0.85
Residual	40	1.12		
Quantum yield				
Per cent canopy openness	1	0.12	5.89	0.02
Invasiveness	1	0.0003	0.17	0.68
Species (invasiveness)	3	0.0008	0.13	0.94
Canopy openness × invasiveness	1	4.0 × 10 ⁻⁶	0.0018	0.96
Canopy openness × species (invasiveness)	3	0.001	0.23	0.87
Residual	40	0.083		
Stomatal conductance				
Per cent canopy openness	1	10.81	99.19	<0.001
Invasiveness	1	0.11	1.01	0.32
Species (invasiveness)	3	3.45	10.53	<0.001
Canopy openness × invasiveness	1	0.31	2.87	0.09
Canopy openness × species (invasiveness)	3	2.25	6.87	<0.001
Residual	40	4.36		
Specific leaf area				
Per cent canopy openness	1	260 188	149.09	<0.001
Invasiveness	1	11 227	6.43	0.015
Species (invasiveness)	3	33 178	6.33	0.001
Canopy openness × invasiveness	1	119	0.068	0.79
Canopy openness × species (invasiveness)	3	4 919	0.93	0.43
Residual	40	69 807		
Water-use efficiency				
Light environment	1	390.43	261.75	<0.001
Invasiveness	1	19.34	12.96	<0.001
Species (invasiveness)	3	9.31	2.08	0.11
Light environment × invasiveness	1	2.18	1.46	0.23
Light environment × species (invasiveness)	3	3.71	0.83	0.48
Residual	40	59.66		

Canopy openness was not measured above plants sampled for water-use efficiency and so light environment was analysed as sun *versus* shade. Summary table indicates degrees of freedom (d.f.), deviance (dev), variance ratios (*F*) and *P*-values (*P*).

higher growth rates because there may be trade-offs in patterns of resource allocation (Poorter & Remkes 1990), but in this study there does appear to be a positive correlation between growth rate and photo-

synthetic rate in *B. darwinii*. Seedlings in full sun had greater probability of survival and were also an order of magnitude larger than seedlings grown in the shade (McAlpine 2005). We did not measure the growth of

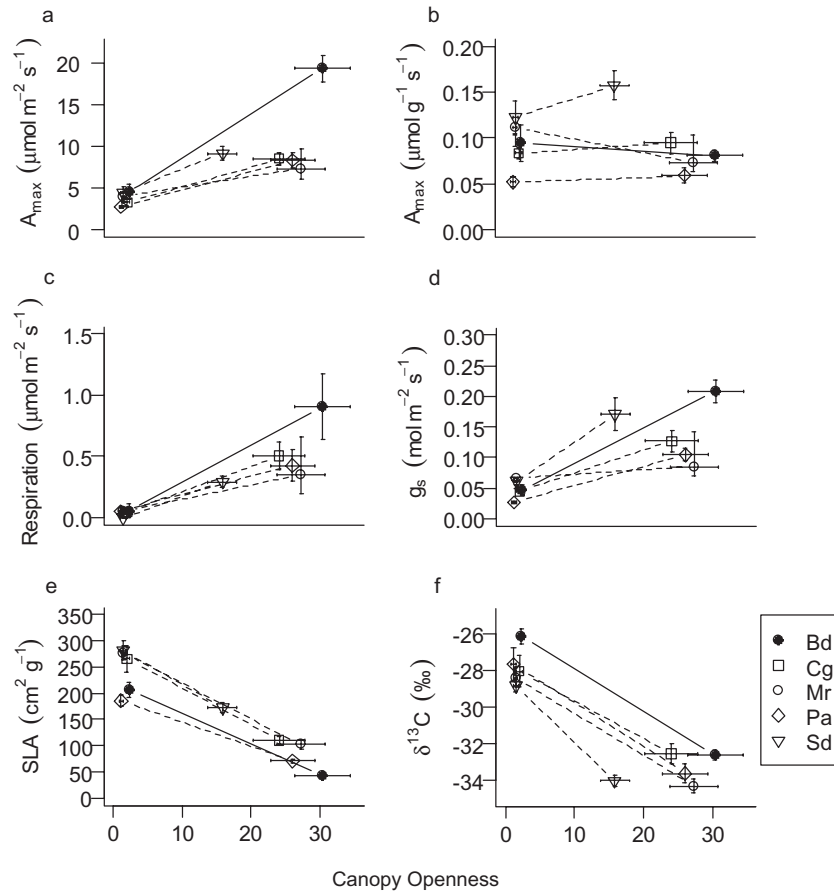


Fig. 4. Photosynthetic measurements from wild plants growing in sun and shade: (a) A_{\max} ; (b) A_{\max} expressed on a per-unit-mass basis; (c) dark respiration; (d) stomatal conductance (g_s); (e) specific leaf area (SLA); and (f) $\delta^{13}\text{C}$. Each bar indicates the mean (± 1 standard error) value from five leaves (one leaf from each of five plants). Canopy openness was not measured above plants sampled for water-use efficiency; however, these plants were in the same area as plants sampled for photosynthetic traits, and so the average canopy openness should be the same. Species are: Bd, *Berberis darwinii*; Cg, *Coprosma grandifolia*; Mr, *Melicactus ramiflorus*; Pa, *Pseudopanax arboreus*; Sd, *Schefflera digitata*.

the native species, largely because of extremely low seedling survival rates, but we did observe that 2-year-old seedlings of *B. darwinii* were at least twice as tall as the 2-year-old seedlings of the four native species in sunny sites. Photosynthetic rates were only higher in *B. darwinii* when expressed as a per-area basis. The lack of differences in photosynthesis when analysed on a per-unit-mass basis suggests that *B. darwinii* responds to high light by allocating more biomass to photosynthesis, rather than increasing the efficiency of the photosynthetic reactions, and indeed, *B. darwinii* seedlings grown in high light allocated significantly more carbon to leaves than those grown in shade (McAlpine & Jesson, 2007).

Consistent with the master-of-some hypothesis, *B. darwinii* does not appear to have a similar carbon-gain advantage under shady conditions. Many species with higher photosynthetic rates in sunny conditions also show higher carbon gain than other plants in shady conditions (e.g. Owens 1996; Pattison *et al.*

1998; Durand & Goldstein 2001b), but *B. darwinii* does not appear to be one of them. Interestingly, despite the fact that we could not detect an obvious competitive advantage in shaded conditions, *B. darwinii* is considered a 'shade-tolerant' weed species (Webb *et al.* 1988; Allen 1991). Its persistence in the shade is likely related to the high germination rate found in unfavourable environments. While only a small percentage of these seedlings survived, more individuals persisted after 18 months than in the other species studied. Darwin's barberry employs a Jack-of-all-trades strategy for germination, and a master-of-some strategy for photosynthesis, resulting in an overall Jack-and-master strategy for invasion success. The numerical advantage in the shade will likely be lost over time, especially if overtopped by surrounding vegetation or if conditions continue to be unfavourable. Long-term studies examining the survival of seedlings to adult plants are needed to fully understand the persistence of *B. darwinii* in the shade.

Greater WUE has previously been proposed as a factor contributing to invasion success, particularly when water is a limiting resource (Busch & Smith 1995; Kloeppel & Abrams 1995; Stratton & Goldstein 2001). In the current study, however, while WUE was higher for *B. darwinii*, it responded to sun and shade in a similar manner as the native species. In addition, measurements of stomatal conductance were higher in the sun but similar in the shade, suggesting that *B. darwinii* responds to high light by opening stomata, which would increase water loss. The greater WUE is therefore not due to strategies that limit the loss of water, but is a result of the greater carbon gain of *B. darwinii*, which more than offsets the increased water loss in the sunny sites. It seems likely that in the sunny sites in this study, water was not a limiting resource. While we were specifically testing the responses of *B. darwinii* to sun and shade environments, favourable and unfavourable situations can constitute a myriad of environmental conditions; traits such as WUE may play a more important role as resources other than light become limiting.

Using a Jack-of-all-trades, master-of-some framework provides a mechanism to understand how plant traits interact to contribute to invasion success. In this study, the germination and survival of seedlings after 18 months closely resembled a Jack-of-all-trades strategy, but area-based estimates of photosynthetic rate showed an advantage only in open-canopy environments, suggesting that with respect to carbon gain, *B. darwinii* is a master-of-some invader. Thus, in *B. darwinii* it is not photosynthetic rate per se that contributes to invasion success, rather the interaction of photosynthetic rate and light environment. This framework in turn provides managers with useful strategies for controlling invaders: in this species efforts should be directed at removing plants in high light, rather than across all environments.

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