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Growth responses and phenotypic plasticity of eight environmental weed species grown from seed in deep shade

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Abstract Shade tolerance is a key factor determining which environmental weeds can invade and persist in intact forest, where light availability can be as low as 1% of full sunlight. Understanding which species can survive under such low light is critical for predicting future invasions. We examined growth responses and phenotypic plasticity of eight environmental weeds: three palms (*Archontophoenix cunninghamiana*, *Phoenix canariensis*, *Trachycarpus fortunei*), four trees (*Acer negundo*, *Maytenus boaria*, *Pinus patula*, *Prunus lusitanica*), and one vine (*Actinidia chinensis*). We used a shade-house experiment with four shade levels (53%, 93%, 97%, 99%) to assess seedling establishment, biomass, root:shoot ratio (R:S), and specific leaf area (SLA). Palms showed high shade tolerance, with minimal variation in establishment and small biomass reductions at the deepest shade, but little plasticity. *Maytenus boaria* and *Prunus lusitanica* were moderately shade tolerant, with stable establishment but larger biomass declines between 97% and 99% shade. *Actinidia chinensis* and *Acer negundo* were less tolerant, showing greater biomass and establishment declines under deep shade. *Pinus patula* was least tolerant, with no seedlings surviving at 99% shade and the greatest biomass reduction between 53% and 93% shade. *Maytenus boaria* and *Actinidia chinensis* showed the greatest plasticity, with declining R:S and increasing SLA with shade. *Prunus lusitanica* was plastic in SLA but not R:S, while *Acer negundo* and *Pinus patula* showed minimal plasticity. Results indicate that all species except for *Pinus patula* have potential to establish in deep shade. Further research to determine their ability to invade intact native forests would be valuable.

Keywords Biomass allocation, invasive plant, leaf traits, light, seedling growth, shade tolerance

INTRODUCTION

The term "shade tolerance" can be defined as the ability of a plant species to survive and develop in shade. Variation in shade tolerance among species is a key factor underlying plant community dynamics and is a primary mechanism driving forest succession following disturbance (Valladares & Niinemets 2008; Poorter et al. 2023).

For environmental weeds – invasive plants that have negative impacts in natural ecosystems – the degree of shade tolerance exhibited by seedlings plays a key role in determining which ecosystems they can invade and how long they can persist (Lugo 2004; Martin et al. 2009). Most environmental weeds are light-demanding and typically establish in disturbed, high-light environments (Martin et al. 2009; Funk 2013), but shade-tolerant invaders pose a greater threat to undisturbed ecosystems because they can potentially establish, survive, and persist under closed-canopy conditions (Lugo 2004; Martin & Marks 2006; Martin et al. 2009) where light levels can be as low as 1% of full sun (Champion 1988; McDonald & Norton 1992; Davies-Colley et al. 2000; Lusk et al. 2009). Some shade-tolerant environmental weeds can form 'seedling banks' in deep shade that remain suppressed for decades until canopy gaps appear (e.g. *Acer platanoides*, Norway maple; Martin & Marks 2006). Shade-tolerant environmental weeds also have the potential to increase in abundance in the understorey, persist

indefinitely (in the absence of disturbance) and have long-term impacts on ecosystem functioning (Meyer & Florence 1996; Martin 1999; Shouman et al. 2017; McAlpine et al. 2021). Conversely, because shade-intolerant environmental weeds tend to die out when they are overtopped by shade-tolerant plant species (whether native or non-native), their impacts can be short-lived. However, shade-intolerant environmental weeds can have persistent impacts when they invade lower-stature plant communities, such as when trees invade grasslands or wetlands (Griffiths & McAlpine 2017; Peltzer 2018).

Phenotypic plasticity, or the ability of a given genotype to express different phenotypes in different environments can contribute to shade tolerance (Gratani 2014; Shouman et al. 2017) and be an important mechanism of plant invasion (Daehler 2003; Richardson & Pyšek 2006; Funk 2008; Davidson et al. 2011; Gioria et al. 2023). According to optimal partitioning models, plant species with high phenotypic plasticity can optimise growth under different environmental conditions by shifting biomass allocation among tissue types (e.g. altering root to shoot (R:S) ratio) to maximise capture of limiting resources (e.g. water or light) (Tilman 1988). Plasticity within tissue types to maximise photosynthetic efficiency under different or changing light levels, may also be advantageous (Schieving & Poorter 1999). For environmental weeds, phenotypic plasticity in traits such as R:S or specific leaf area (SLA) could confer an extra competitive advantage if, for example, that plasticity enabled survival in a wide range of habitat types, or greater agility in responding to environmental change (Pattison et al. 1998; Yamashita et al. 2003; Richards et al. 2006; Avalos 2019; Poorter et al. 2023). However, plasticity comes at a cost; for example, adjusting to different environmental conditions requires energy that might otherwise be used for growth and reproduction (Valladares et al. 2007; Liu et al. 2016; Schneider 2022).

We conducted a shade-house experiment to quantify and compare seedling establishment and growth responses of eight environmental weed species grown in the low-light levels typical of intact New Zealand forests. The eight species were chosen because they are considered emerging weeds by New Zealand weed experts; species that are not yet widespread but have the potential to become invasive and problematic in the future. These weeds are typically identified based on: their ability to spread rapidly; outcompete native vegetation; and cause significant ecological harm. Shade-tolerant species pose an additional risk because they have potential to invade intact (undisturbed) native forest, so this was an additional criterion used to select study species; seven of the eight study species are reported to be moderately to highly shade tolerant (Table 1). The eighth species (*Pinus patula*) is shade-intolerant (Niinemets et al. 2006), making it a useful control for comparison. We hypothesised that species with greater plasticity in root-to-shoot ratio (R:S) and specific leaf area (SLA) will show smaller reductions in growth (total biomass) with increasing shade.

MATERIALS AND METHODS

Study species

We chose eight emerging environmental weed species that are established, but not yet widespread, in New Zealand. All species have considerable potential for range expansion, including into native forests and other natural ecosystems. Seven of the eight study species are reported to be moderately to highly shade tolerant and the eighth species (*Pinus patula*) is reported to be shade-intolerant (Table 1). Taxonomy follows the Global Biodiversity Information Facility Taxonomic Backbone (GBIF Secretariat 2024). All eight species were included on the 2024 list of environmental weeds in New Zealand (McAlpine & Howell 2024).

Acer negundo L. (box elder) is a deciduous tree, native to North and Central America from Canada to Honduras. It is ranked among the 40 most invasive woody species of the world (Rejmánek & Richardson 1996) and has been recorded as introduced or invasive in 52 countries (ISSG 2024). It is tolerant of shade, heat and water stress (Saccone et al. 2010a; Sikorska et al. 2019) and has become one of the most invasive plant species in riparian forests in Europe (Khapugin 2019; Sikorska et al. 2019). Seeds are dispersed by wind and water, so there is high potential for relatively rapid spread of this species, particularly in riparian communities.

Actinidia chinensis Planch. (kiwifruit) is a bird-dispersed woody vine, native to China and recorded as introduced or invasive in 14 countries (ISSG 2024). Kiwifruit has been described as light-demanding (Poorter et al. 2019) but also moderately shade tolerant (Sullivan & Williams 2002). Wild kiwifruit vines can form dense, heavy blankets that smother and collapse native vegetation and interfere with natural regeneration (Sullivan et al. 2006). Kiwifruit Vine Health (KVH), the national organisation that supports the New Zealand kiwifruit industry, recognises this and puts considerable resources into managing wild kiwifruit seedlings.

Archontophoenix cunninghamiana (H.Wendl.) H.Wendl. & Drude (Bangalow palm) is a cold-sensitive, shade- and drought-tolerant palm tree, native to the east coast of New South Wales and Queensland in Australia, and recorded as introduced or invasive in six countries (ISSG 2024). Seeds are dispersed by birds and water. Seedlings and juveniles can persist for years in the shady forest understorey (Bello et al. 2021) and can shade out and displace native species, including the native nikau palm (*Rhopalostylis sapida*) in New Zealand (Global Invasive Species Database 2024a).

Maytenus boaria Molina (maiten) is an evergreen large shrub or small tree, native to Chile and Argentina and recorded as introduced or invasive in New Zealand and the USA (ISSG 2024). Seeds are dispersed by birds, and this species also spreads aggressively by root suckers (Heenan et al. 1999). Hardy, shade tolerant and cold tolerant, this species has been described as a 'ticking time-bomb' with potential for explosive spread throughout New Zealand (Dawson 2016).

Table 1. Shade tolerance of the eight study species according to published literature. Reported shade tolerance categories are as described (largely anecdotally) in the studies cited. Interpretation of terminology: 'light-demanding' or 'shade-intolerant' = low shade tolerance, 'shade-tolerant' or 'moderately shade tolerant' = moderate shade tolerance, 'extremely', 'very', 'strongly' or 'highly' shade tolerant = high shade tolerance. Niinemets and Valladares (2006) use a five-level scale for shade tolerance: 1, very intolerant; 2, intolerant; 3, moderately tolerant; 4, tolerant; 5, very tolerant.

Species	Species abbreviation used in figures	Common name	Reported shade tolerance	References
Acer negundo L.	ACEneg	box elder	moderate to high	Rosario (1988); Niinemets and Valladares (2006, tolerance score 3.47±0.1); Saccone et al. (2010a); Saccone et al. (2010b)
Actinidia chinensis Planch.	ACTchi	kiwifruit	low to moderate	Sullivan and Williams (2002); Poorter et al. (2019)
Archontophoenix cunninghamiana (H.Wendl.) H.Wendl. & Drude	ARCcun	Bangalow palm	moderate to high	Bello et al. (2021); Global Invasive Species Database (2024a)
Maytenus boaria Molina	MAYboa	maiten	moderate to high	Renison et al. (2011); Dawson (2016)
Phoenix canariensis H.Wildpret	PHOcan	Phoenix palm	moderate	Global Invasive Species Database (2024b)
Pinus patula Schiede ex Schltdl. & Cham.	PINpat	Mexican weeping pine	low	Gillespie (1992); Niinemets et al. (2006)
Prunus lusitanica L.	PRUlus	Portuguese laurel	low to moderate	Arévalo and Fernández-Palacios (1998); Niinemets and Valladares (2006, tolerance score 2.5); Pulido et al. (2008)
Trachycarpus fortunei (Hook.) H.Wendl.	TRAfor	Chinese windmill palm	high	Koike (2006); Fehr and Burga (2016)

Phoenix canariensis H.Wildpret (Phoenix palm) is a large palm tree, native to the Canary Islands and recorded as introduced or invasive in 20 countries (ISSG 2024). It tolerates a wide range of conditions (cold and warm, drought and floods, sun and shade, salt spray) and has been extensively cultivated in warm temperate regions around the world. Seeds are dispersed by birds and water. It is capable of invading native bush and displacing native species, and its long, sharp spines can cause injury to humans and animals.

Pinus patula Schiede ex Schltdl. & Cham. (Mexican weeping pine) is a large, wind-dispersed tree, native to eastern Mexico and recorded as introduced or invasive in 32 countries (ISSG 2024). It has been a widely planted timber crop and is now one of the most widespread invasive pine species globally (Richardson 1998). *Pinus patula* is reported to be shade intolerant, as is the case with most *Pinus* species (Poorter et al. 2019).

Prunus lusitanica L. (Portuguese laurel) is a bird-dispersed, medium-sized evergreen tree, native to the Iberian Peninsula, Morocco, the Macronesian archipelagos, and the French Basque Country. This species has been described as shade-tolerant in its native range (Arévalo & Fernández-Palacios 1998; Pulido et al. 2008) but also intolerant of deep shade. It has been recorded as introduced or invasive in seven countries (ISSG 2024).

Trachycarpus fortunei (Hook.) H.Wendl. (Chinese windmill palm) is a bird-dispersed, cold- and shade-tolerant palm tree native to parts of China, Japan, Myanmar and India. It is one of the most invasive palms worldwide (Fehr et al. 2020) and has been recorded as introduced or invasive in 11 countries (ISSG 2024). *Trachycarpus fortunei* can form dense stands, with juveniles persisting for many years in the understorey, shading out native understorey species (Ishii & Iwasaki 2008).

Study site

This experiment was conducted in outdoor shade-houses at the Bioeconomy Science Institute AgResearch Group site at Ruakura, Hamilton, New Zealand (latitude -37.776745, longitude 175.308974, 45 m a.s.l.). Mean annual rainfall is 1142.1 mm and mean annual air temperature is 14.3 °C (mean daily max. 19.8 °C, mean daily min. 8.9 °C) (1991–2024 data from Ruakura climate station[1]).

Shade-houses

Twelve shade-houses were constructed to create three replicates of four shade treatments. Each shade-house was made from four plastic crates fixed together to give overall dimensions of 408 cm wide × 100 cm deep × 83 cm high. Shade-houses were covered with a wooden frame made from 4 × 9 cm timber, measuring 440 cm wide × 130 cm deep × 220 cm high. Frames were then covered with different combinations of low-, medium-, and high-density green polyethylene garden shade-cloth to create different shade levels. To determine which shade-cloth combinations

[1] Data obtained 22 October 2024 from the National Institute of Water & Atmosphere's (NIWA's) National Climate Database using the CliFlo web tool http://cliflo.niwa.co.nz. The database is now accessible via Earth Sciences New Zealand's DataHub https://data.niwa.co.nz/pages/clidb-on-datahub

would achieve the desired shade levels, the amount of light reduced by each shade-cloth treatment was measured using a LI-COR® LI-1500 light sensor logger and a LI-COR® light sensor inside and outside each shade-house. Photosynthetic photon flux density (the amount of photosynthetically active photons reaching the light sensor) was measured once per second for five minutes per shade-house. The average percent shade created by each shade-cloth treatment was calculated by comparing the amount of light inside the shade-house with the amount of light outside the shade-house (see below).

Our aim was to test seedling establishment and growth responses in deep shade at levels typically found under closed canopy native podocarp-broadleaf forest in New Zealand. Shade levels in this type of forest are generally above 90% shade, reaching up to 99% shade (McDonald & Norton 1992; Young & Mitchell 1994; Davies-Colley et al. 2000; Coomes et al. 2005; Lusk et al. 2009). Accordingly, we chose to test seedling responses to three shade levels above 90%, plus a control of approximately 50% shade. To create these four shade levels, we used a single layer of medium density shade-cloth (53.26% shade ± 0.59%, mean ± s.d.), low + high density shade-cloth (93.19% shade ± 0.67%), medium + high density shade-cloth (96.54% shade ± 0.39%) and high + high density shade-cloth (98.59% shade ± 0.12%). We note that the low variability in light levels within the shade-houses might be due to the use of a single sensor for measurements, which may have prevented the capture of spatial variability. This unmeasured spatial variability could blur the boundaries between treatments, potentially making the differences between them not significant, so results should be interpreted with caution. Hereafter, these shade levels are rounded to 53%, 93%, 97%, and 99%. We chose to test these extreme shade levels because most of our study species are reported to be moderately to highly shade tolerant and we wanted to push them to their limits. While the differences in seedling responses between 93%, 97%, and 99% shade are unlikely to be as pronounced as those between lower shade levels, they can still provide valuable insights into the shade tolerance and adaptability of different species. We selected 50% shade as the control to minimise potential confounding effects of reduced soil moisture, which are more likely to occur in full sun or light shade. This decision was based on a pilot study that tested seedling responses to 0%, 20%, and 50% shade and above (KGM, unpublished data).

Seed sowing substrate

Crates were filled with untreated topsoil to a depth of ~50 cm. A 10-cm layer of potting mix was added on top to prevent unwanted weed seed emergence from the topsoil giving a total substrate depth of ~60 cm.

Seed collection and sowing

Seed collection locations and dates varied by species (Table 2). Fruits were collected from a minimum of seven plants per species. Kiwifruit seeds were retrieved from twenty kiwifruits purchased at a supermarket. For fleshy-fruited species, fruit pulp was manually removed, then seeds were spread out to dry at room temperature. Seeds were sown

Table 2. Seed collection, seed sowing and seedling harvesting information.

Species	Seed collection areas/sources	Date seeds collected	Date seeds sown	Number of seeds sown per cell	Date seedlings harvested	Number of months between seed sowing and harvest
Acer negundo L.	Christchurch, Thames, Hamilton, Gisborne	April 2021	May 2021	50	Feb 2022	9
Actinidia chinensis Planch.	Wellington supermarket	May 2021	June 2021	100	Feb 2022	8
Archontophoenix cunninghamiana (H.Wendl.) H.Wendl. & Drude	Thames, Hamilton	April 2021	May 2021	50	Nov 2022	18
Maytenus boaria Molina	Christchurch	April 2021	May 2021	100	Feb 2022	9
Phoenix canariensis H.Wildpret	Thames	April 2021	May 2021	50	May 2022	12
Pinus patula Schiede ex Schltdl. & Cham.	Hotoritori	May 2021	Feb 2022*	45	Nov 2022	9
Prunus lusitanica L.	Christchurch, Blackball, Omakau	April 2021	May 2021	50	May 2022	12
Trachycarpus fortunei (Hook.) H.Wendl.	Christchurch, Thames, Hamilton	April 2021	May 2021	50	Nov 2022	18

**Pinus patula* seeds were stored at ~4° C for 9 months and sown when another species failed to germinate.

fresh (not stratified) as soon as practical, to replicate the timing of naturally dispersed seeds in the field. However, the lack of stratification may have resulted in low and delayed or uneven germination rates.

To divide the shade-house soil surface into seed-sowing 'cells', each of the four crates within each shade-house was divided into quarters. This gave a total of sixteen 50 × 58 cm cells per shade-house laid out on an 8 × 2 cell grid. Each species was randomly allocated two cells, one per side, within each shade-house, giving a total of 24 cells per species. The number of seeds sown per species varied due to seed size and availability at time of collection (Table 2).

Cells were kept uniformly moist by supplementing rainfall with overhead sprinklers and hand-watering. Slug bait was applied as needed.

Seedling growth and harvest

Emerging seedlings were thinned (removed) or transplanted when necessary, so that seedlings were evenly spaced throughout the cell with a minimum of 2 cm between seedlings. Thinning was only required for *Actinidia chinensis* (mean 4.5 ± 5.9 seedlings removed per cell) and *M. boaria* (mean 57.8 ± 6.7 seedlings removed per cell). Thinned seedlings were removed from seedling establishment calculations: *a/(b-c)* where *a* = number of seedlings present at time of harvest, *b* = number of seeds sown, and *c* = number of seedlings thinned. Note that this calculation assumes all seeds were viable, which is unlikely. Consequently, percent seedling establishment may be under-estimated, as the number of seeds sown (*b*) would be lower if unviable seeds were excluded. Cells were weeded periodically to remove seedlings of unwanted species that emerged.

The length of time between seed sowing and seedling harvest varied by species (Table 2). The decision to harvest a species was made when at least some seedlings were: (a) becoming tall or wide enough to impinge on neighbouring cells; or (b) growth appeared to have stalled (i.e. plant height and width did not appear to have changed much in several months). At time of harvest, all remaining seedlings were counted and then harvested.

The ten largest plants from each cell – or all plants, if less than ten survived to the end – were used for growth metrics (Figure 1). Note that this sampling methodology may have introduced biases in the results, as it does not account for the role of density dependence in shaping seedling responses across shade treatments (Weiner et al. 2001). For instance, less-crowded seedlings, which grow with fewer constraints, may exhibit more homogeneity in size. Conversely, more crowded seedlings could experience greater competition, potentially resulting in increased size variability. On the other hand, selecting the largest plants ensures the data represents the most successful growth outcomes and helps to minimise the impact of outliers and extreme variations.

Soil was carefully washed off the roots of the ten largest plants, then each plant was separated into above-ground (shoot) and below-ground (root) biomass by cutting stems at soil surface level (determined during harvest). Shoot length was measured to the top of the newest developing leaf whorl, and root length was measured to the bottom of the main root branch. To calculate SLA (leaf area per unit leaf mass), one fully expanded leaf (or part of a leaf) was removed from the five biggest plants in each cell. Leaf area was then measured using a LI-COR LI-3100C leaf-area meter. All plant material was placed in paper bags and oven-dried at 80°C for approximately 48 hours, or up to 96 hours for very large plants. After drying, plant material was weighed and SLA and root:shoot ratio (R:S) calculated.

Statistical analyses

We analysed the effect of shade on seedling establishment, seedling biomass, root:shoot ratio and SLA separately for each species. Seedling establishment was modelled using generalised linear mixed-effects models (GLMMs) with a binomial response variable of successes (the number of seedlings harvested per cell) and failures (the number of seeds sown minus the number of seedlings thinned per cell), shade as a categorical fixed effect (with four levels), and shade-house as a random effect. To account for overdispersion, we compared the binomial model to an observation-level random effect binomial model and a beta-binomial model (Harrison 2015), using: Akaike Information Criterion corrected for small sample size (AICc); AICc weights (probability of the model being the best in this set of candidate models); and inspection of residual plots to select the best model (Akaike 1974; Hurvich & Tsai 1989; Burnham & Anderson 2002). The binomial model was the best model for all species, except for *Actinidia chinensis* where the beta-binomial model was the best model. We inspected residual plots of the best models to assess whether model assumptions were met, and there were no concerning patterns.

We modelled total biomass, R:S and SLA using gamma GLMMs with a log link function to ensure model estimates were always positive (Zuur & Ieno 2016). All models had shade as a categorical fixed effect and cell nested within shade-house as random effects, except for *Phoenix canariensis* SLA where including shade-house as a random effect resulted in model convergence issues, so only cell was included as a random effect. We inspected residual plots and ran model diagnostic tests for all models to assess whether model assumptions were met. For *Actinidia chinensis*, one extremely small seedling caused models to fit poorly, so was removed from the data. For several models, residuals varied among levels of shade. To account for heteroscedasticity in these models, we added a dispersion parameter that modelled residual variance as a function of shade (Brooks et al. 2017). For some models, there were patterns in the residuals even after adding the dispersion parameter (total biomass: *Acer negundo* and *Actinidia chinensis*; SLA: *Acer negundo*, *Archontophoenix cunninghamiana* and *T. fortunei*), significant deviance (SLA: *T. fortunei*), or outliers (R:S: *M. boaria*; SLA: *Archontophoenix cunninghamiana* and *Prunus lusitanica*), although variance among residuals was reduced (except for *Actinidia chinensis* biomass, where the dispersion parameter was removed from the final model) and model predictions were still a good fit to the data.

Models were fitted using the glmmTMB package (Brooks et al. 2017) in R 4.3.3 (R Core Team 2024). We used the DHARMa package (Hartig 2022) to create scaled residual plots using a simulation approach and to run model

Figure 1. Harvested seedling bunches tied with coloured ribbon arranged from left to right by increasing shade level: 53%, 93%, 97%, and 99%. In lieu of a scale to indicate relative seedling sizes, the above-ground height of the tallest seedling recorded for each species is as follows: *Acer negundo* 140 cm; *Actinidia chinensis* 166 cm; *Archontophoenix cunninghamiana* 28 cm, *Maytenus boaria* 95 cm; *Phoenix canariensis* 56 cm, *Pinus patula* 31 cm; *Prunus lusitanica* 58 cm; *Trachycarpus fortunei* 31 cm.

diagnostic tests. The AICc values and AICc weights were calculated using the MuMIn package (Barton 2022). For each model, pairwise contrasts were used to compare all shade levels using estimated marginal means derived from the fitted model, with Tukey adjusted P-values for multiple comparisons, using the emmeans package (Lenth 2022). We plotted model-based estimates for all response variables (on the response scale) for each shade level using predictions calculated in the ggeffects package (Lüdecke 2018).

RESULTS

No seedlings of *Pinus patula* survived at 99% shade, so total biomass, R:S and SLA data were analysed for 53%, 93% and 97% shade levels only. For most species, seedling establishment did not differ among shade levels (Figure 2). However, fewer *Acer negundo* seedlings established at 99% shade than at 53%, and *Actinidia chinensis* seedling establishment was lower at 99% shade than at all other shade levels.

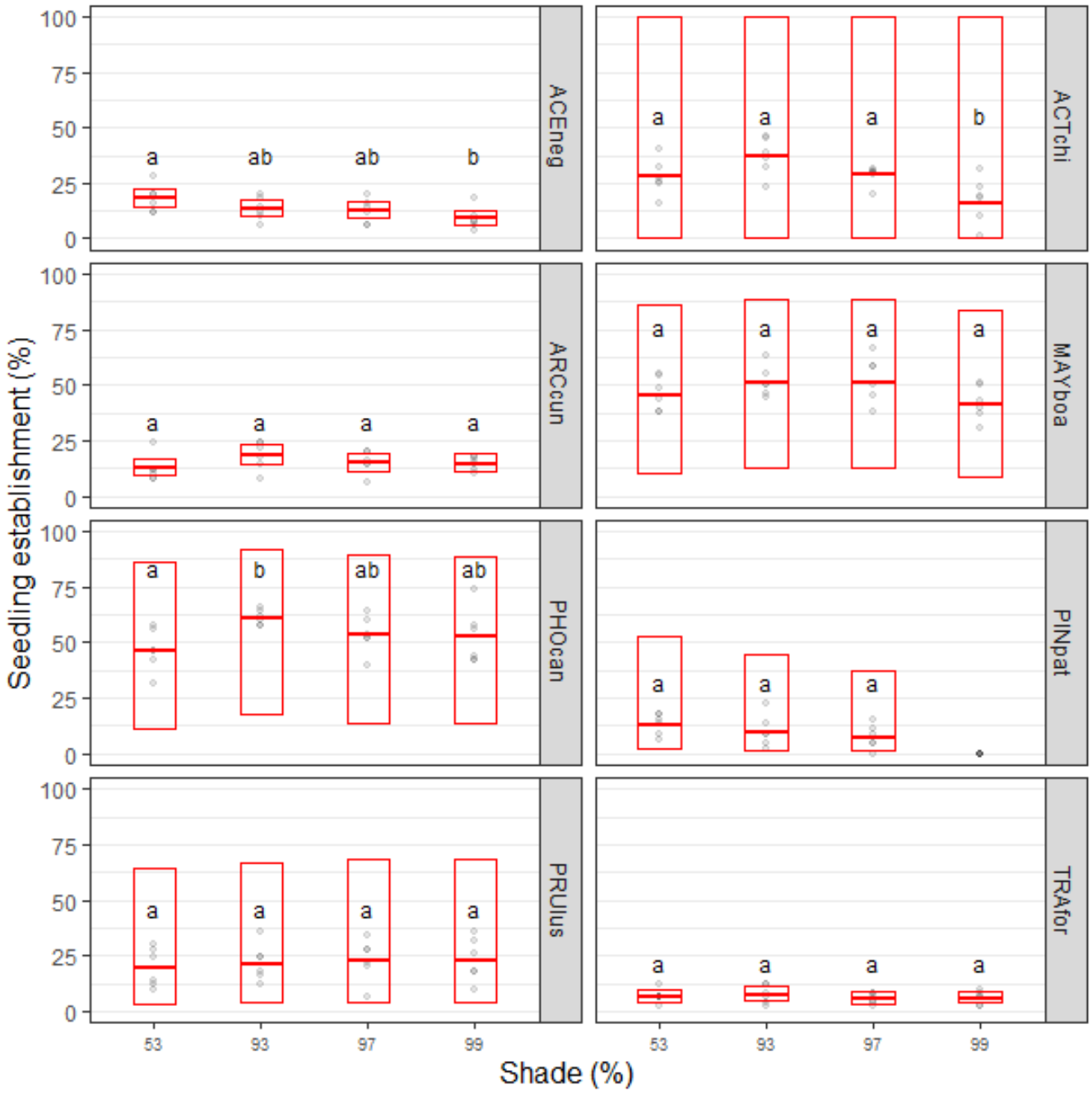

Figure 2. Effect of shade on observed (points) and predicted (boxes, backtransformed mean ± 95% model prediction intervals) seedling establishment for eight environmental weed species. Letters indicate statistically significant differences. See Table 1 for species abbreviations.

For all species, total biomass was higher for seedlings grown at 53% shade than at all the deep shade levels (93%, 97% and 99%; Figures 1 and 3). Total biomass also differed among all the deep shade levels, with seedlings becoming progressively smaller at deeper shade (93% > 97% > 99% for all species; Figures 1 and 3). Differences in seedling biomass were greater among deep shade levels than between 53% and 93% for all species except for *Pinus patula*, but especially so for *Acer negundo*, *Actinidia chinensis* and *M. boaria* (and *Prunus lusitanica* to a lesser extent), where there was a large decline in biomass between 97% and 99% shade (Figure 3). For *Pinus patula*, differences in seedling biomass were greater between 53% and 93% shade than 93% and 97%.

For all species except *Pinus patula* and *Prunus lusitanica*, seedling R:S was greater at 53% shade than at all the deep shade levels (Figure 4). In deep shade, *M. boaria* was the only species that also had consistently greater R:S at less shady levels than in deeper shade (93% > 97% > 99%) (Figure 4). *Actinidia chinensis* R:S was also higher at 93% than 99% shade, but there was no difference detected between 93% and 97%, or 97% and 99% shade (Figure 4). For *Archontophoenix cunninghamiana* and *Phoenix canariensis*,

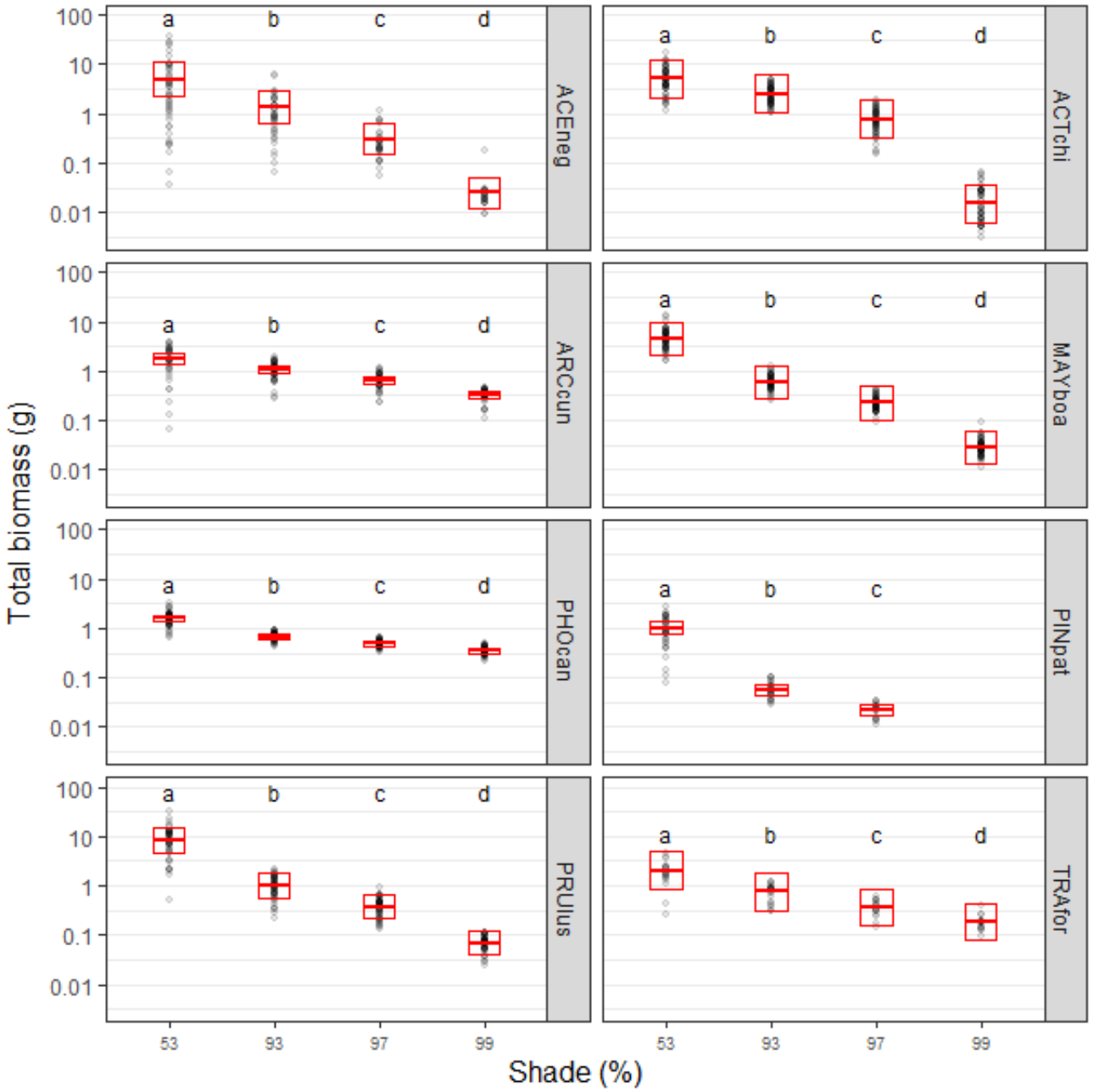

Figure 3. Effect of shade on observed (points) and predicted (boxes, backtransformed mean ± 95% model prediction interval) seedling total biomass for eight environmental weed species. Note the y-axis is on a log scale. Letters indicate statistically significant differences. See Table 1 for species abbreviations.

R:S was greater at the deepest shade level (99%) than at 93% and 97% shade (Figure 4). For *Acer negundo* and *T. fortunei*, R:S did not differ among deeper shade levels (Figure 4). *Pinus patula* R:S was greater at 93% than 97% shade (Figure 4). *Prunus lusitanica* R:S mostly did not differ among shade levels, except for a lower ratio at 93% shade than at 53% or 97% (Figure 4).

For all species except *Pinus patula*, SLA was lower at 53% shade than at all deeper shade levels (Figure 5). For *Actinidia chinensis*, *Archontophoenix cunninghamiana* and *M. boaria*, SLA also increased between each of the deepest shade levels (93% < 97% < 99%) (Figure 5). A similar pattern was seen for *Phoenix canariensis* and *Prunus lusitanica*, although there was no difference in SLA between 93% and 97% shade for either species (Figure 5). *Acer negundo* SLA was lower at 99% shade than at 97% (Figure 5). *Trachycarpus fortunei* SLA did not differ among any of the deeper shade levels, and there was no difference in SLA among any of the shade levels for *Pinus patula* seedlings (Figure 5).

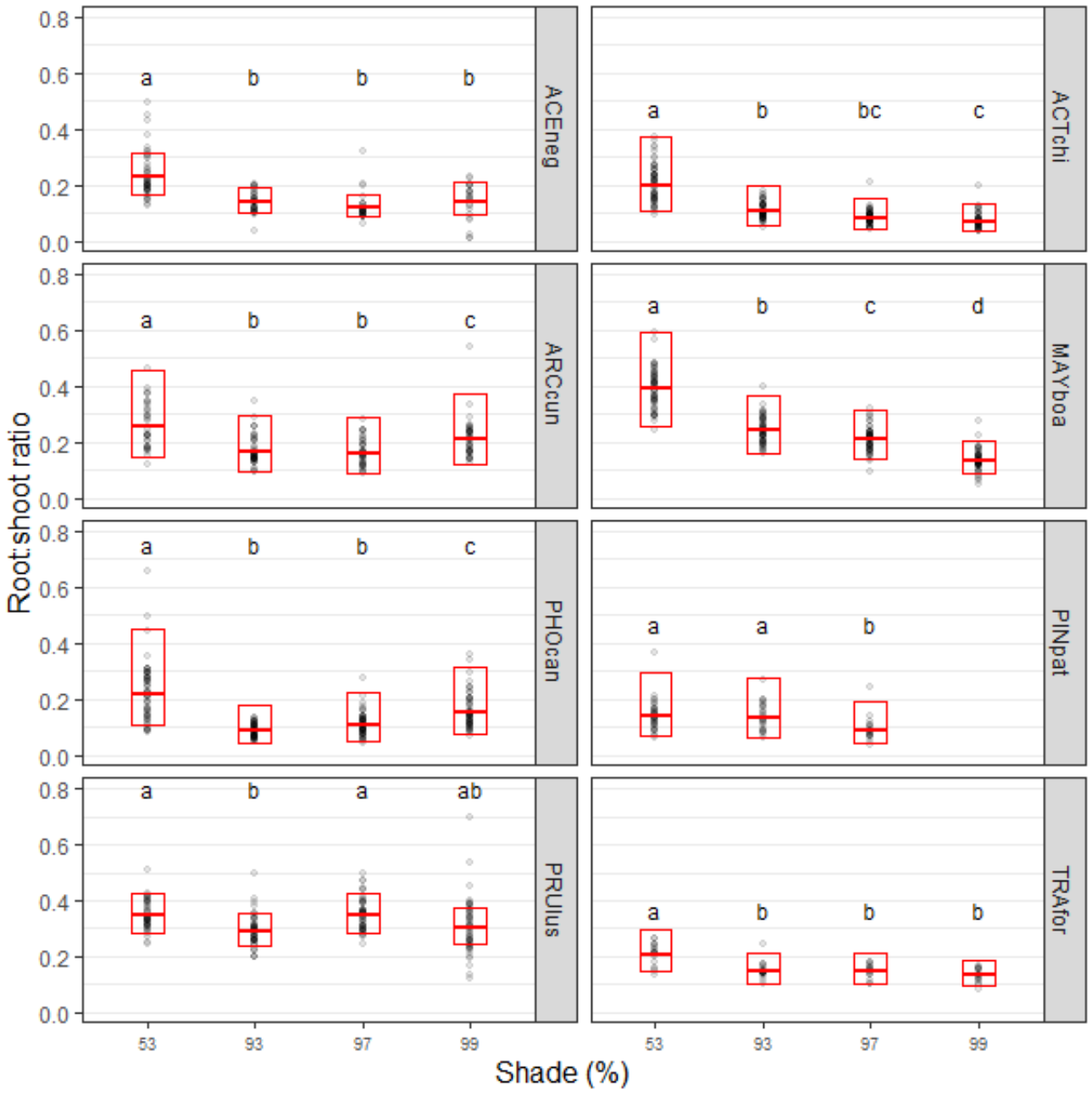

Figure 4. Effect of shade on observed (points) and predicted (boxes, backtransformed mean ± 95% model prediction interval) seedling root:shoot ratio for eight environmental weed species. Letters indicate statistically significant differences. See Table 1 for species abbreviations.

DISCUSSION

This study provides insight into the shade tolerance and phenotypic plasticity of eight environmental weeds, contributing to our understanding of their potential to invade intact native forest in New Zealand where light levels can be as low as 1-5% of full sun (McDonald & Norton 1992; Young & Mitchell 1994; Davies-Colley et al. 2000; Coomes et al. 2005; Lusk et al. 2009). Significant differences in all metrics, depending on species, confirm that a mere 2% reduction in available light from 97% shade to 99% shade can have a major effect on seedling growth and establishment.

Highly shade-tolerant environmental weeds, such as the three palm species (*Archontophoenix cunninghamiana*, *Phoenix canariensis*, and *Trachycarpus fortunei*), are particularly concerning due to their potential ability to invade intact, closed canopy native forest and persist in the understorey for decades or longer (Valladares et al. 2016). The three palm species had similar growth patterns, with minimal variation in seedling establishment and relatively small reductions in biomass between the two highest shade levels. These results indicate a strong ability to tolerate deep shade, although this does not appear to be

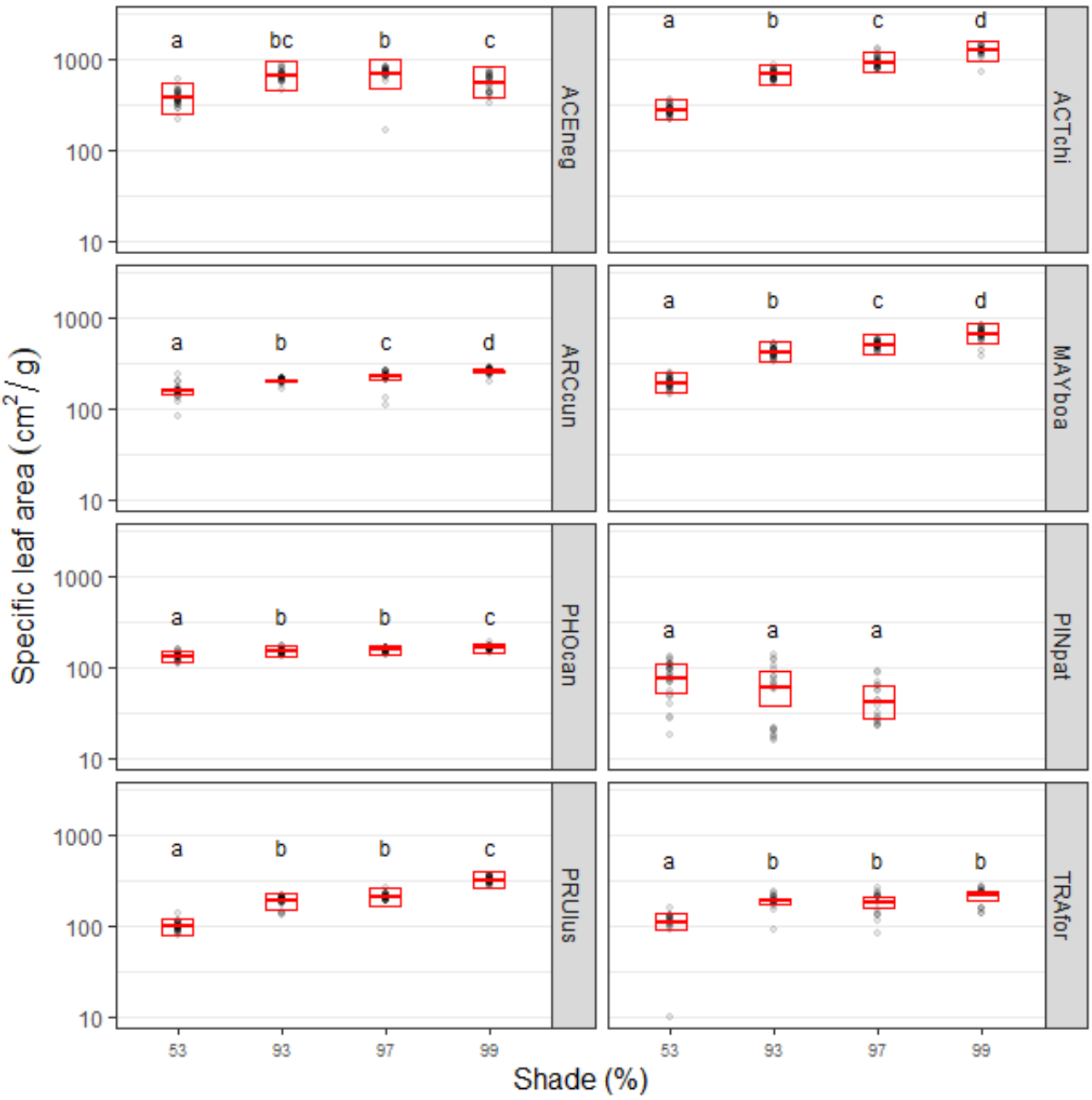

Figure 5. Effect of shade on observed (points) and predicted (boxes, backtransformed mean ± 95% model prediction interval) seedling specific leaf area (SLA) for eight environmental weed species. Note the y-axis is on a log scale. Letters indicate statistically significant differences. See Table 1 for species abbreviations.

due to plasticity in biomass allocation. *Phoenix canariensis* exhibited the highest seedling establishment rates, ranging from 46–62% across shade levels, indicating its capacity for widespread invasion. Conversely, *T. fortunei* had the lowest establishment rates (5–8%), potentially due to lower seed viability or other suboptimal conditions, such as the need for cold stratification to germinate.

Conversely, *Pinus patula* was the least shade-tolerant species (as expected), with minimal phenotypic plasticity and no seedlings surviving under 99% shade. While such shade-intolerant environmental weeds may dominate disturbed, high-light environments, they are likely to be outcompeted by shade-tolerant species in naturally forested ecosystems as succession proceeds. However, light is not the only factor that can affect successional processes; other site-specific factors such as climate, allelopathy or the presence of grazing animals can play a major role (Connell & Slatyer 1977; Poorter et al. 2023). In New Zealand, shade-tolerant native species often colonise the understorey of closed-canopy *Pinus* spp. forests (including *Pinus patula*, KGM pers. obs.) and it has been suggested that in the absence of disturbance, native species may replace the pines completely at these sites (Brockerhoff et al. 2003; McAlpine et al. 2018; McAlpine et al. 2021).

Acer negundo, *Actinidia chinensis*, *M. boaria* and *Prunus lusitanica* demonstrated moderate shade tolerance. For both *Acer negundo* and *Actinidia chinensis*, biomass declined with increasing shade, particularly between 97% and 99%, and seedling establishment was reduced at 99% shade. Also, the reversal of trend in SLA for *Acer negundo* at 99% shade suggests that seedlings were struggling under extreme shade and may not have survived if the experiment had run for longer. Similarly, *Prunus lusitanica* exhibited declining biomass and increasing SLA with shade but showed little plasticity in R:S ratio, indicating a relatively fixed biomass allocation strategy among tissue types. *Maytenus boaria* and *Actinidia chinensis* displayed the highest degree of phenotypic plasticity, as evidenced by a consistent decline in root-to-shoot ratio (R:S) and an increase in SLA across all shade levels, which suggests that these species may be capable of acclimating to a range of habitats and light environments. Although *Actinidia chinensis* is only moderately shade tolerant, its rapid growth and climbing ability may enable it to invade relatively intact forests by quickly escaping the low-light conditions of the forest floor and reaching the canopy.

Our findings mostly align with previous studies on the shade tolerance of the eight species we studied (Table 1). However, we cannot be sure that seedlings of these species will respond to shade in the same way in the field, because the homogenous, relatively benign conditions in the shade-houses were likely very different to the heterogenous, variable conditions that seedlings experience in the field, particularly at the seedling scale (McAlpine & Drake 2002). Stressors such as pests and pathogens, drought, wind, mechanical damage, and competition with other plant species that would typically reduce seedling establishment in the field were mostly controlled in the shade-houses, so greatly reduced stress on seedlings perhaps led to greater establishment in deep shade than would be possible in the field. Despite these favourable conditions, for all species except the three palms, seedlings growing in 99% shade were extremely small and likely would not have survived much longer. Clarifying how long seedlings of the study species can survive under different (or changing) shade levels in the field would be a useful focus of future research.

When exposed to shade, most plant species will optimise light capture and utilisation by increasing SLA to some extent (Evans & Poorter 2001), so it was not surprising that SLA of most study species was higher at 99% shade than at 53% shade. More interesting was the fact that three species (*Actinidia chinensis*, *Archontophoenix cunninghamiana* and *M. boaria*) had an increase in SLA as shade increased across all shade levels, including the tiny 2% increase in shade between 97% and 99% shade, indicating a very sensitive response mechanism to low light. However, the ability to compensate for low light by increasing SLA doesn't necessarily translate into a growth or survival advantage. For example, large, thin leaves (i.e. with a high SLA) can be sensitive to mechanical stress and herbivory, which can have negative consequences for plant survival in shade (Augspurger 1984; Gamage 2011). SLA is a complex trait, often related to plant size and leaf longevity, and is part of a broader network of traits within the leaf economics spectrum, which collectively influence a plant's strategy for growth and survival (Reich 2014; Onoda et al. 2017; Fajardo & Siefert 2018).

Our results do not support our hypothesis that species with greater plasticity in root-to-shoot ratio (R:S) and specific leaf area (SLA) will show smaller reductions in growth (total biomass) with increasing shade. In fact, the two most phenotypically plastic species (*M. boaria* and *Actinidia chinensis*) showed relatively large declines in biomass with increasing shade compared to species lacking phenotypic plasticity in R:S and SLA. This suggests that plasticity does not prevent declines in biomass with increasing shade – at least for these two species. It may also be indicative of other underlying factors influencing growth responses to shade that are not accounted for by plasticity in R:S and SLA (Xu et al. 2021; Sellaro et al. 2025).

Artificial experiments such as ours do not capture the broader role that plasticity might play in the establishment, distribution and persistence of environmental weeds in the wild (Hulme 2008). Patterns of biomass allocation – and even shade tolerance itself – can be affected by environmental conditions, so the minimum light availability tolerated by any given species may vary in different ecosystems or sites (Valladares & Niinemets 2008; Poorter 2009). Additionally, shade tolerance and trait plasticity can change as plants age (Fetcher et al. 1994; McConnaughay & Coleman 1999; Lusk et al. 2008). Nevertheless, our results extend current knowledge regarding the shade tolerance of these significant environmental weeds.

Management implications

Seedling shade tolerance is an important consideration when determining environmental weed management priorities. Shade-tolerant environmental weeds such as the three palm species may be able to invade intact (undisturbed) native forest communities, which means they can have

severe negative impacts at sites with high biodiversity values. *Trachycarpus fortunei* is unusually cold-tolerant compared to other palm tree species (Reichgelt et al. 2018), so likely poses a greater invasion risk in colder areas of New Zealand than *Phoenix canariensis* and *Archontophoenix cunninghamiana*. Warming temperatures will likely allow all three palm species to spread south, with studies predicting considerable expansion of suitable habitat under climate change for both *Archontophoenix cunninghamiana* (Sheppard 2013) and *T. fortunei* (Aguilar et al. 2017).

Environmental weeds with shade-tolerant seedlings may also be able to regenerate under their own canopy, replacing adult plants as they die and thereby potentially persisting in perpetuity (McAlpine et al. 2021). Shade tolerant environmental weeds should be a priority for management and control in native forest, particularly where seed sources are present, and managers should be on the alert for seedling establishment of these species in otherwise minimally disturbed forest.

Conversely, in areas that support native forest, shade-intolerant environmental weeds such as *Pinus patula* tend to die out as succession proceeds because they are unable to regenerate in the increasingly shady understorey (Williams 2011; McAlpine et al. 2021). This means that their impacts can be shorter lived and less severe than shade-tolerant environmental weeds, and they typically pose less of a threat to established forest ecosystems. However, shade-intolerant environmental weeds can still have major impacts where they invade following disturbance, dominating invaded sites for the life of adult plants, which may be decades or even centuries for long-lived species such as *Pinus patula* and other wilding conifers. Furthermore, when woody environmental weeds invade naturally treeless ecosystems such as wetlands, grasslands and alpine habitats impacts can be severe and irreversible (Rundle et al. 2014), regardless of seedling shade tolerance. In New Zealand, invasions of wilding conifers into grasslands and willows into low-stature wetlands are pertinent examples of such transformative effects (Griffiths & McAlpine 2017; Peltzer 2018).

CONCLUSIONS

The range of shade tolerance and plasticity displayed by the eight study species underscores the need for tailored management approaches to mitigate the ecological impacts of environmental weeds. Effective management strategies should prioritise control of shade-tolerant environmental weeds in minimally disturbed forests while also managing shade-intolerant environmental weeds in open or edge habitats. Future research of the study species should focus on the long-term survival and ecological interactions under field conditions to inform conservation efforts.

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REFERENCES

Aguilar GD, Blanchon DJ, Foote H, Pollonais CW, Mosee AN 2017. A performance based consensus approach for predicting spatial extent of the Chinese windmill palm (*Trachycarpus fortunei*) in New Zealand under climate change. Ecological Informatics 39: 130-139. https://doi.org/10.1016/j.ecoinf.2017.04.004

Akaike H 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19: 716-723. https://doi.org/10.1109/TAC.1974.1100705

Arévalo JR, Fernández-Palacios JM 1998. Treefall gap characteristics and regeneration in the laurel forest of Tenerife. Journal of Vegetation Science 9: 297-306. https://doi.org/10.2307/3237094

Augspurger CK 1984. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. Journal of Ecology 72: 777-795. https://doi.org/10.2307/2259531

Avalos G 2019. Shade tolerance within the context of the successional process in tropical rain forests. Revista de Biologia Tropical 67: 1-25. https://doi.org/10.15517/rbt.v67i2SUPL.37206

Barton K 2022. MuMIn: multi-model inference. R package version 1.46.0.

Bello C, Cintra ALP, Barreto E, Vancine MH, Sobral-Souza T, Graham CH, Galetti M 2021. Environmental niche and functional role similarity between invasive and native palms in the Atlantic Forest. Biological Invasions 23: 741-754. https://doi.org/10.1007/s10530-020-02400-8

Brockerhoff EG, Ecroyd CE, Leckie AC, Kimberley MO 2003. Diversity and succession of adventive and indigenous vascular understorey plants in *Pinus radiata* plantation forests in New Zealand. Forest Ecology and Management 185: 307-326. https://doi.org/10.1016/S0378-1127(03)00227-5

Brooks ME, Kristensen K, Van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Machler M, Bolker BM 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9: 378-400. https://doi.org/10.32614/RJ-2017-066

Burnham KP, Anderson DR 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edn. New York, Springer. 488 p.

Champion PD 1988. The ecology and management of kahikatea *Dacrycarpus dacrydioides* (A. Rich) de Laubenfels in the Waikato, North Island, New Zealand, Masters Thesis. University of Waikato.

Connell JH, Slatyer RO 1977. Mechanisms of succession in natural communities and their role in community stability and organization. The American Naturalist 111: 1119-1144. https://doi.org/10.1086/283241

Coomes DA, Allen RB, Bentley WA, Burrows LE, Canham CD, Fagan L, Forsyth DM, Gaxiola-Alcantar A, Parfitt RL, Ruscoe WA 2005. The hare, the tortoise and the crocodile: the ecology of angiosperm dominance, conifer persistence and fern filtering. Journal of Ecology 93: 918-935. https://doi.org/10.1111/j.1365-2745.2005.01012.x

Daehler CC 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. Annual Review of Ecology Evolution and Systematics 34: 183-211. https://doi.org/10.1146/annurev.ecolsys.34.011802.132403

Davidson AM, Jennions M, Nicotra AB 2011. Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. Ecology Letters 14: 419-431. https://doi.org/10.1111/j.1461-0248.2011.01596.x

Davies-Colley RJ, Payne GW, van Elswijk M 2000. Microclimate gradients across a forest edge. New Zealand Journal of Ecology 24: 111-121.

Dawson M 2016. Chilean mayten (*Maytenus boaria*) - a ticking time-bomb? New Zealand Garden Journal 19: 28-32.

Evans JR, Poorter H 2001. Photosynthetic acclimation of plants to growth irradiance: the relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. Plant, Cell & Environment 24: 755-767. https://doi.org/10.1046/j.1365-3040.2001.00724.x

Fajardo A, Siefert A 2018. Intraspecific trait variation and the leaf economics spectrum across resource gradients and levels of organization. Ecology 99: 1024-1030. https://doi.org/10.1002/ecy.2194

Fehr V, Burga C 2016. Aspects and causes of earlier and current spread of *Trachycarpus fortunei* in the forests of southern Ticino and northern Lago Maggiore (Switzerland, Italy). Palms 60: 125-136.

Fehr V, Buitenwerf R, Svenning JC 2020. Non-native palms (Arecaceae) as generators of novel ecosystems: A global assessment. Diversity and Distributions 26: 1523-1538. https://doi.org/10.1111/ddi.13150

Fetcher N, Oberbauer SF, Chazdon RL 1994. Physiological ecology of plants. In: McDade LA, Bawa KS, Hespenheide HA, Hartshorn GS Ed. La Selva: ecology and natural history of a neotropical rain forest. Chicago and London, The University of Chicago Press. Pp. 128-141.

Funk JL 2008. Differences in plasticity between invasive and native plants from a low resource environment. Journal of Ecology 96: 1162-1173. https://doi.org/10.1111/j.1365-2745.2008.01435.x

Funk JL 2013. The physiology of invasive plants in low-resource environments. Conservation Physiology 1: 1-17. https://doi.org/10.1093/conphys/cot026

Gamage HK 2011. Phenotypic variation in heteroblastic woody species does not contribute to shade survival. AoB Plants 2011 plr013. https://doi.org/10.1093/aobpla/plr013

GBIF Secretariat 2024. GBIF Backbone Taxonomy. Checklist dataset https://doi.org/10.15468/39omei accessed via GBIF.org on 10 October 2024.

Gillespie AJ 1992. *Pinus patula* Schiede and Deppe. Patula pine. Pinaceae. Pine family. USDA Forest Service, Southern Forest Experiment Station, Institute of Tropical Forestry. 5 p. (SO-ITF-SM; 54).

Gioria M, Hulme PE, Richardson DM, Pyšek P 2023. Why are invasive plants successful? Annual Review of Plant Biology 74: 635-670. https://doi.org/10.1146/annurev-arplant-070522-071021

Global Invasive Species Database 2024a. Species profile: *Archontophoenix cunninghamiana*. Downloaded from http://www.iucngisd.org/gisd/species.php?sc=1665 on 24-09-2024.

Global Invasive Species Database 2024b. Species profile: *Phoenix canariensis*. Downloaded from http://www.iucngisd.org/gisd/speciesname/Phoenix+canariensis on 26-09-2024.

Gratani L 2014. Plant phenotypic plasticity in response to environmental factors. Advances in Botany 2014: 1-17. https://doi.org/10.1155/2014/208747

Griffiths JW, McAlpine KG 2017. Aerial glyphosate application reduces grey willow (*Salix cinerea*) canopy cover, increases light availability, and stimulates kahikatea (*Dacrycarpus dacrydioides*) growth. New Zealand Journal of Ecology 41: 234-239. https://doi.org/10.20417/nzjecol.41.22

Harrison XA 2015. A comparison of observation-level random effect and Beta-Binomial models for modelling overdispersion in Binomial data in ecology & evolution. PeerJ 3: e1114. https://doi.org/10.7717/peerj.1114

Hartig F 2022. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R Package version 0.4.6. https://CRAN.R-project.org/package=DHARMa.

Heenan PB, de Lange PJ, Glenny DS, Breitwieser I, Brownsey PJ, Ogle CC 1999. Checklist of dicotyledons, gymnosperms, and pteridophytes naturalised or casual in New Zealand: additional records 1997-1998. New Zealand Journal of Botany 37: 629-642. https://doi.org/10.1080/0028825X.1999.9512658

Hulme PE 2008. Phenotypic plasticity and plant invasions: is it all Jack? Functional Ecology 22: 3-7. https://doi.org/10.1111/j.1365-2435.2007.01369.x

Hurvich CM, Tsai C-L 1989. Regression and time series model selection in small samples. Biometrika 76: 297-307. https://doi.org/10.1093/biomet/76.2.297

Ishii HT, Iwasaki A 2008. Ecological restoration of a fragmented urban shrine forest in southeastern Hyogo Prefecture, Japan: Initial effects of the removal of invasive *Trachycarpus fortunei*. Urban Ecosystems 11: 309-316. https://doi.org/10.1007/s11252-008-0067-6

ISSG 2024. Invasive Species Specialist Group. Global Register of Introduced and Invasive Species (GRIIS). https://griis.org. Accessed 21 October 2024.

Khapugin AA 2019. A global systematic review of publications concerning the invasion biology of four tree species of temperate Eurasia. Hacquetia 18: 233-270. https://doi.org/10.2478/hacq-2019-0005

Koike F 2006. Invasion of an alien palm (*Trachycarpus fortunei*) into a large forest. In: Koike F, Clout MN, Kawamichi M, De Poorter M, Iwatsuki K Ed. Assessment and control of biological invasion risks. Kyoto, Japan and IUCN, Gland, Switzerland, Shoukadoh Book Sellers. Pp. 200-203.

Lenth RV 2022. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.7.2. https://CRAN.R-project.org/package=emmeans.

Liu Y, Dawson W, Prati D, Haeuser E, Feng Y, van Kleunen M 2016. Does greater specific leaf area plasticity help plants to maintain a high performance when shaded? Annals of Botany 118: 1329-1336. https://doi.org/10.1093/aob/mcw180

Lugo AE 2004. The outcome of alien tree invasions in Puerto Rico. Frontiers in Ecology and the Environment 2: 265-273. https://doi.org/10.1890/1540-9295(2004)002[0265:TOOATI]2.0.CO;2

Lusk C, Falster DS, Jara-Vergara C, Jimenez-Castillo M, Saldaña-Mendoza A 2008. Ontogenetic variation in light requirements of juvenile rainforest evergreens. Functional Ecology 22: 454-459. https://doi.org/10.1111/j.1365-2435.2008.01384.x

Lusk CH, Duncan RP, Bellingham PJ 2009. Light environments occupied by conifer and angiosperm seedlings in a New Zealand podocarp-broadleaved forest. New Zealand Journal of Ecology 33: 83-89.

Martin PH 1999. Norway maple (*Acer platanoides*) invasion of a natural forest stand: understory consequence and regeneration pattern. Biological Invasions 1: 215-222. https://doi.org/10.1023/A:1010084421858

Martin PH, Marks PL 2006. Intact forests provide only weak resistance to a shade-tolerant invasive Norway maple (*Acer platanoides* L.). Journal of Ecology 94: 1070-1079. https://doi.org/10.1111/j.1365-2745.2006.01159.x

Martin PH, Canham CD, Marks PL 2009. Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. Frontiers in Ecology and the Environment 7: 142-149. https://doi.org/10.1890/070096

McAlpine KG, Drake DR 2002. The effects of small-scale environmental heterogeneity on seed germination in experimental treefall gaps in New Zealand. Plant Ecology 165: 207-215. https://doi.org/10.1023/A:1022247707932

McAlpine KG, Timmins SM, Jackman SD, Lamoureaux SL 2018. Composition of the understory in 132 woody weed populations and implications for succession. New Zealand Journal of Ecology 42: 277-283. https://doi.org/10.20417/nzjecol.42.33

McAlpine KG, Lamoureaux SL, Timmins SM 2021. Understory vegetation provides clues to succession in woody weed stands. New Zealand Journal of Ecology 45: 1-10. https://dx.doi.org/10.20417/nzjecol.45.4

McAlpine KG, Howell CJ 2024. List of environmental weeds in New Zealand 2024. Science for Conservation 340. Wellington, Department of Conservation Te Papa Atawhai. 37 p.

McConnaughay KDM, Coleman JS 1999. Biomass allocation in plants: ontogeny or optimality? A test along three resource gradients. Ecology 80: 2581-2593. https://doi.org/10.1890/0012-9658(1999)080[2581:BAIPOO]2.0.CO;2

McDonald D, Norton DA 1992. Light environments in temperate New Zealand podocarp rainforests. New Zealand Journal of Ecology 16: 15-22.

Meyer J-Y, Florence J 1996. Tahiti's native flora endangered by the invasion of *Miconia calvescens* DC. (Melastomataceae). Journal of Biogeography 23: 775-781. https://doi.org/10.1111/j.1365-2699.1996.tb00038.x

Niinemets Ü, Tobias M, Cescatti A, Sparrow A 2006. Size-dependent variation in shoot light-harvesting efficiency in shade-intolerant conifers. International Journal of Plant Sciences 167: 19-32. https://doi.org/10.1086/497845

Niinemets Ü, Valladares F 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. Ecological Monographs 76: 521-547. https://doi.org/10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2

Onoda Y, Wright IJ, Evans JR, Hikosaka K, Kitajima K, Niinemets Ü, Poorter H, Tosens T, Westoby M 2017. Physiological and structural tradeoffs underlying the leaf economics spectrum. New Phytologist 214: 1447-1463. https://doi.org/10.1111/nph.14496

Pattison RR, Goldstein G, Ares A 1998. Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. Oecologia 117: 449-459. https://doi.org/10.1007/s004420050680

Peltzer DA 2018. Ecology and consequences of invasion by non-native (wilding) conifers in New Zealand. Journal of New Zealand Grasslands 80: 39-46. https://doi.org/10.33584/jnzg.2018.80.359

Poorter H, Niinemets Ü, Ntagkas N, Siebenkäs A, Mäenpää M, Matsubara S, Pons T 2019. A meta-analysis of plant responses to light intensity for 70 traits ranging from molecules to whole plant performance. New Phytologist 223: 1073-1105. https://doi.org/10.1111/nph.15754

Poorter L 2009. Leaf traits show different relationships with shade tolerance in moist versus dry tropical forests. New Phytologist 181: 890-900. https://doi.org/10.1111/j.1469-8137.2008.02715.x

Poorter L, Amissah L, Bongers F, Hordijk I, Kok J, Laurance SG, Lohbeck M, Martínez-Ramos M, Matsuo T, Meave JA 2023. Successional theories. Biological Reviews 98: 2049-2077. https://doi.org/10.1111/brv.12995

Pulido F, Valladares F, Calleja JA, Moreno G, González-Bornay G 2008. Tertiary relict trees in a Mediterranean climate: abiotic constraints on the persistence of *Prunus lusitanica* at the eroding edge of its range. Journal of Biogeography 35: 1425-1435. https://doi.org/10.1111/j.1365-2699.2008.01898.x

R Core Team 2024. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Reich PB 2014. The world-wide 'fast-slow'plant economics spectrum: a traits manifesto. Journal of Ecology 102: 275-301. https://doi.org/10.1111/1365-2745.12211

Reichgelt T, West CK, Greenwood DR 2018. The relation between global palm distribution and climate. Scientific Reports 8: 4721. https://doi.org/10.1038/s41598-018-23147-2

Rejmánek M, Richardson DM 1996. What attributes make some plant species more invasive? Ecology 77: 1655-1661. https://doi.org/10.2307/2265768

Renison D, Hensen I, Suarez R 2011. Landscape structural complexity of high-mountain *Polylepis australis* forests: a new aspect of restoration goals. Restoration Ecology 19: 390-398. https://doi.org/10.1111/j.1526-100X.2009.00555.x

Richards CL, Bossdorf O, Muth NZ, Gurevitch J, Pigliucci M 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. Ecology Letters 9: 981-993. https://doi.org/10.1111/j.1461-0248.2006.00950.x

Richardson DM 1998. Forestry trees as invasive aliens. Conservation Biology 12: 18-26. https://doi.org/10.1111/j.1523-1739.1998.96392.x

Richardson DM, Pyšek P 2006. Plant invasions: merging the concepts of species invasiveness and community invasibility. Progress in Physical Geography 30: 409-431. https://doi.org/10.1191/0309133306pp490pr

Rosario LC 1988. *Acer negundo*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). https://www.fs.usda.gov/database/feis/plants/tree/aceneg/all.html. Accessed 27 September 2024.

Rundle PW, Dickie IA, Richardson DM 2014. Tree invasions into treeless areas: mechanisms and ecosystem processes. Biological Invasions 16: 663-675. https://doi.org/10.1007/s10530-013-0614-9

Saccone P, Brun J-J, Michalet R 2010a. Challenging growth-survival trade-off: a key for *Acer negundo* invasion in European floodplains? Canadian Journal of Forest Research 40: 1879-1886. https://doi.org/10.1139/X10-134

Saccone P, Pagès JP, Girel J, Brun JJ, Michalet R 2010b. *Acer negundo* invasion along a successional gradient: early direct facilitation by native pioneers and late indirect facilitation by conspecifics. New Phytologist 187: 831-842. https://doi.org/10.1111/j.1469-8137.2010.03289.x

Schieving F, Poorter H 1999. Carbon gain in a multispecies canopy: the role of specific leaf area and photosynthetic nitrogen-use efficiency in the tragedy of the commons. The New Phytologist 143: 201-211. https://doi.org/10.1046/j.1469-8137.1999.00431.x

Schneider HM 2022. Characterization, costs, cues and future perspectives of phenotypic plasticity. Annals of Botany 130: 131-148. https://doi.org/10.1093/aob/mcac087

Sellaro R, Durand M, Aphalo PJ, Casal JJ 2025. Making the most of canopy light: shade avoidance under a fluctuating spectrum and irradiance. Journal of Experimental Botany 76: 712-729. https://doi.org/10.1093/jxb/erae334

Sheppard CS 2013. Potential spread of recently naturalised plants in New Zealand under climate change. Climatic Change 117: 919-931. https://doi.org/10.1007/s10584-012-0605-3

Shouman S, Mason N, Kichey T, Closset-Kopp D, Heberling JM, Kobeissi A, Decocq G 2017. Functional shift of sycamore maple (*Acer pseudoplatanus*) towards greater plasticity and shade tolerance in its invasive range. Perspectives in Plant Ecology, Evolution and Systematics 29: 30-40. https://doi.org/10.1016/j.ppees.2017.11.001

Sikorska D, Sikorski P, Archiciński P, Chormański J, Hopkins RJ 2019. You can't see the woods for the trees: Invasive *Acer negundo* L. in urban riparian forests harms biodiversity and limits recreation activity. Sustainability 11: 5838. https://doi.org/10.3390/su11205838

Sullivan JJ, Williams PA 2002. The ecology, distribution, and environmental weed potential of wild kiwifruit (*Actinidia* species) in the Bay of Plenty, New Zealand. Landcare Research Contract Report LC 0102/166

prepared for Environment B.O.P., Whakatane, New Zealand. 37 p.

Sullivan JJ, Stahel W, Mather J Control of wild kiwifruit (*Actinidia* species) in Bay of Plenty, New ZealandPp. 583-590. https://doi.org/10.17660/ActaHortic.2007.753.77

Tilman D 1988. Plant strategies and the dynamics and structure of plant communities. Princeton, USA, Princeton University Press. 360 p. https://doi.org/10.1515/9780691209593

Valladares F, Gianoli E, Gómez JM 2007. Ecological limits to plant phenotypic plasticity. New phytologist 176: 749-763. https://doi.org/10.1111/j.1469-8137.2007.02275.x

Valladares F, Niinemets U 2008. Shade tolerance, a key plant feature of complex nature and consequences. Annual Review of Ecology, Evolution, and Systematics 39: 237-257. https://doi.org/10.1146/annurev.ecolsys.39.110707.173506

Valladares F, Laanisto L, Niinemets Ü, Zavala MA 2016. Shedding light on shade: ecological perspectives of understorey plant life. Plant Ecology & Diversity 9: 237-251. https://doi.org/10.1080/17550874.2016.1210262

Weiner J, Stoll P, Muller-Landau H, Jasentuliyana A 2001. The effects of density, spatial pattern, and competitive symmetry on size variation in simulated plant populations. The American Naturalist 158: 438-450. https://doi.org/10.1086/321988

Williams PA 2011. Secondary succession through non-native dicotyledonous woody plants in New Zealand. New Zealand Natural Sciences 36: 73-91.

Xu H, Chen P, Tao Y 2021. Understanding the shade tolerance responses through hints from phytochrome a-mediated negative feedback regulation in shade avoiding plants. Frontiers in Plant Science 12: 813092. https://doi.org/10.3389/fpls.2021.813092

Yamashita N, Tanaka N, Hoshi Y, Kushima H, Kamo K 2003. Seed and seedling demography of invasive and native trees of subtropical Pacific islands. Journal of Vegetation Science 14: 15-24. https://doi.org/10.1111/j.1654-1103.2003.tb02123.x

Young A, Mitchell N 1994. Microclimate and vegetation edge effects in a fragmented podocarp-broadleaf forest in New Zealand. Biological Conservation 67: 63-72. https://doi.org/10.1016/0006-3207(94)90010-8

Zuur AF, Ieno EN 2016. Beginner's guide to zero-inflated models with R. Newburgh, United Kingdon, Highland Statistics Ltd. 414 p.