Seedling establishment of the invasive tree *Acer pseudoplatanus* (sycamore)

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Summary *Acer pseudoplatanus* L. (sycamore) is a fast-growing tree that is invasive in many parts of the world, including New Zealand and Australia. The aim of this field experiment was to investigate the seedling establishment requirements of sycamore, in order to better predict where invasion is likely to occur. Sycamore seeds were sown into four different light environments in secondary native forest, ranging from full sun to deep shade, and also into a closed-canopy sycamore forest. The percentage of seed germination was calculated nine months after sowing, and seedling survival was calculated 16 months later. The average percent seed germination was similar across all light environments. However, seedling survival was highly variable: 60–70% in the full sun and edge plots, 25% in the native understory plots, and 0% in the sycamore and deep shade plots. These results indicate that sycamore seedlings establish most successfully under high light conditions. They do not establish well in deep shade or in closed canopy sycamore forest, which means they are unlikely to form an extensive seedling/sapling bank. Accordingly, in the absence of disturbance, sycamore could eventually be replaced by native succession in some areas of New Zealand.

Keywords Invasive species, germination, seedling survival, native succession.

INTRODUCTION

Seedling establishment is a key stage of plant invasion. If managers want to predict where invasion is likely to occur, they need to be able to predict where seedlings of that species could establish. Seedling establishment is influenced by overstorey composition and structure through modifications of resource availability (light, water and soil nutrients), along with a wide range of other biotic and abiotic characteristics (Veblen 1992). Understanding the seedling establishment requirements of an invasive species is also useful in predicting long-term population dynamics. In particular, it is critical to know if seedlings can establish beneath the parent (conspecific) canopy. If they do, the ‘seedling bank’ formed may comprise the next successional stage following senescence of the parent trees, thus enabling the invasive species to persist indefinitely. If they do not, then shade-tolerant native species could establish and eventually replace invasive species in the long term.

Acer pseudoplatanus (sycamore, or sycamore maple, Sapindaceae) is a large, deciduous tree, native to central Europe and south-western Asia. It is fast growing, relatively shade-tolerant, and produces copious amounts of wind-dispersed seed. It was originally introduced to New Zealand *c.* 1880, and is now common in many modified habitats including abandoned gardens, waste land, scrub bordering roadsides, rivers in gullies, and stands of secondary and regenerating forest (Webb *et al*. 1988). It is also invasive in many other countries including Australia, the United States of America, the United Kingdom, Sweden and Norway. In New Zealand, it forms dense, monospecific stands, and is reported anecdotally to have a range of negative effects on indigenous ecosystems and vegetation. Congeners *A. platanoides* L. and *A. negundo* L. are highly invasive in Europe and North America and have been extensively studied there (e.g. Martin 1999, Porté *et al*. 2011), but studies on *A. pseudoplatanus* in its invasive range appear to be scarce. One observational study from New Zealand suggested that sycamore could invade short stature native woody vegetation, but not beech (*Nothofagus*) forest (Williams 2009).

The purpose of this study was to test sycamore seedling establishment in a range of native forest light environments, in order to identify where invasion might occur. Additionally, sycamore seedling establishment in closed-canopy sycamore forest was tested in order to assess the likelihood of a second generation of sycamore seedlings establishing beneath the parent canopy. This information is useful in assessing the long-term persistence of this invasive species.

MATERIALS AND METHODS

Study site This study was conducted within Zealandia, a 249 ha ecological restoration site in Wellington, New Zealand (41° 18.3’ S, 174° 44.8’ E). Mean annual rainfall is 1249 mm, and mean annual temperature is 12.8°C (NIWA, 2014). The predominant vegetation is regenerating evergreen broadleaf/podocarp forest, with patches of exotic trees including sycamore and *Pinus radiata* D.Don. This experiment was set up as part of a broader research project; for further details regarding the study site and methods, see McAlpine *et al*. (2008).

Experimental design In order to establish the influence of different light environments on sycamore seed germination and seedling establishment, four site types were chosen on the basis of canopy cover: full sun, edge, understory, deep shade. Full sun sites were located near the centre of artificial treefall gaps. These gaps were created when patches of 3–4 exotic *Pinus radiata* were felled for an earlier research project (see McAlpine and Drake 2003). Edge sites were located on the sunniest edge of the treefall gaps, understory sites were located in areas of undisturbed native forest, and the deep shade sites were located beneath tall, dense native forest, close to the shady side of a hill. A fifth type of site, 'sycamore', was located in closed-canopy stands of sycamore forest. Three replicates of each site type were chosen, giving a total of 15 sites.

Seed sowing At each of the 15 sites, three replicate plots of 1 m^2 were established, giving a total of 45 plots. Plots were cleared, levelled, and covered with 1 cm of heat-sterilised forest soil. In March 2001, 20 sycamore seeds were sown onto each plot, and covered with a thin layer of leaf litter. Soil, leaf litter, and most seeds were collected from within Zealandia, with additional seeds collected from neighbouring suburbs. A sheet of 1 cm metal mesh was placed over the plots for the first three months to prevent seed displacement by birds. Percent canopy openness was quantified at each plot using hemispherical photography and Gap Light Analyser software. Seedlings were counted approximately six weekly, from the time they began germinating in August 2001, until January 2002. Percent germination was estimated by taking the maximum number of seedlings counted during this period. This method does not account for seedlings that have emerged and died during the census period, so can only be considered an estimate of percent germination. Seedling survival as a proportion of percent germination was calculated by counting remaining seedlings in January 2003.

Statistical analyses One way ANOVA was used to examine differences in canopy openness across sites, with site as predictor and canopy openness as response variable, followed by multiple pairwise comparisons (Bonferroni-corrected). Linear regression was used to examine the correlation between canopy openness and both germination and survival, with canopy openness as predictor and germination or survival as response variables. One way ANOVA was used to examine differences in germination and survival across sites, with site as predictor and germination or survival as response variables, followed by multiple pairwise comparisons (Bonferroni-corrected).

RESULTS

There was a significant difference in canopy openness between sites (Table 1). As expected, average (± s.e.) percent canopy openness was highest in the full sun sites (38 ± 2), lowest in the sycamore (7 ± 1) and deep shade (9 ± 1) sites, and intermediate in the edge (19 ± 1) and understory (14 ± 2) sites. Pairwise comparisons indicated the following differences in canopy openness between sites: (site types followed by the same capital letter were not significantly different from each other): full sun A, edge B, understory BC, deep shade C, sycamore C. There was no correlation between canopy openness and seed germination ($y = -0.35x + 59.31$, $r^2 = 0.04$), and average percent germination was similar across all sites (Table 1, Figure 1). However, there was

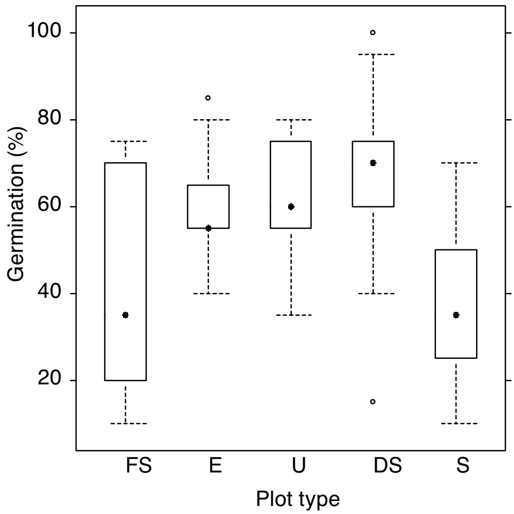

Figure 1. Sycamore seed germination in different plot types (FS = full sun, E = edge, U = understory, DS = deep shade, S = sycamore). Although ANOVA indicated a significant difference (P = 0.03) between plot types, post-hoc pairwise comparisons did not detect how they differed.

Table 1. ANOVA results of response variables canopy openness (CANOPY), percent seed germination (GERM) and seedling survival (SURV) in different plot types (df = 4), ***P <0.001, *P <0.05.

	Sum of squares	Mean square	*F*	P
CANOPY	7342.8	1835.7	103.7	***
GERM	5242.2	1310.6	2.9	*
SURV	41622.0	10405.5	16.6	***

a significant, positive correlation between seedling survival and canopy openness ($y = 1.84x - 1.72$, $r^2 = 0.41$); seedlings only survived in the three highest light environments (Table 1, Figure 2). When two potential outliers were removed, the correlation between seedling survival and canopy openness strengthened further ($y = 2.50x - 9.33$, $r^2 = 0.64$).

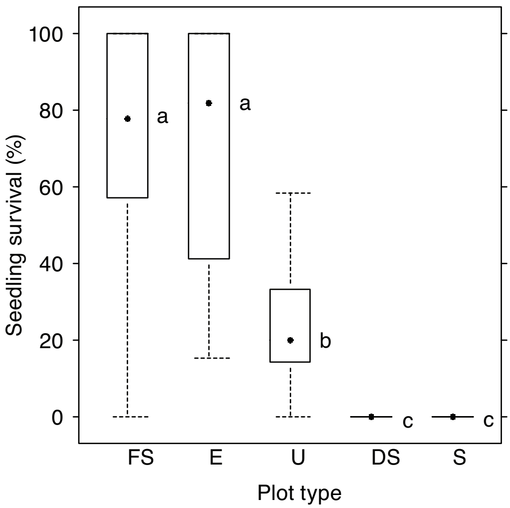

Figure 2. Sycamore seedling survival in different plot types (FS = full sun, E = edge, U = understory, DS = deep shade, S = sycamore). Boxes that share the same letter are not significantly different from each other ($P<0.05$).

DISCUSSION

The shade-tolerance of sycamore seedlings appears to be debatable, with some authors suggesting that sycamore does form a seedling bank beneath the parent canopy, and others describing it as a 'gap species' that cannot colonise closed canopy forest (Leslie 2005). However, the current study indicates that first-year seedlings are not tolerant of deep shade. Coupled with the fact that sycamore is typically found in disturbed habitat, it seems reasonable to conclude that sycamore is not particularly shade tolerant as a young seedling under New Zealand conditions. It may be more shade tolerant as a juvenile or adult plant, as is the case for other invasive woody species such as *Berberis darwinii* Hook. (McAlpine 2005). However, in general, it appears that disturbed or short-stature vegetation is likely to be most at risk from sycamore invasion in New Zealand, as has been suggested by Williams (2009).

Once established, dense sycamore is assumed to have negative impacts on native vegetation, although the nature, severity, and mechanisms underlying these impacts are not well documented. Anecdotal reports from overseas suggest that sycamore displaces natives by casting dense shade, and this may also be the case in New Zealand. Native vegetation in New Zealand is almost exclusively evergreen, so the deciduous nature of sycamore may also change conditions in other ways that are detrimental to native vegetation, such as increasing leaf litter loads and changing rates of nutrient cycling (Vogt *et al*. 1986). Shade also tends to be positively correlated with plant pathogen load, which may further increase seedling mortality in shade (Augspurger and Kelly 1984).

The current study also suggests that sycamore is not likely to establish an extensive seedling bank beneath the parent canopy. Again, this is likely because sycamore seedlings are not sufficiently shade-tolerant to cope with the low light levels present beneath a sycamore canopy. This is good news for managers of this invasive species, particularly since sycamore does not form a persistent seed bank (Dickie *et al.* 1991). Providing the sycamore canopy is not disturbed in the interim, a subsequent generation of sycamore seedlings is not likely to establish until the adult trees senesce. If a subcanopy of native vegetation is able to establish beneath the sycamore canopy before the sycamore senesces, then the next generation is likely to be native. Certainly there are many shade-tolerant native plant species in New Zealand that are capable of establishing beneath exotic forest canopies. In one study from New Zealand, sycamore was shown to be faster growing, but less shade-tolerant, than 12 woody native species (Williams and Buxton 1989). In the current study, a diverse native understory did appear to be establishing beneath the sycamore canopy (K.G. McAlpine pers. obs.). In summary, in the absence of disturbance, it appears that native vegetation could eventually replace sycamore forest naturally in New Zealand.

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