

RESEARCH ARTICLE

Better left alone: Trying to control pasture grasses in untended rainforest plantings incurs multiple costs and delivers few benefits

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Abstract

1. Rainforest revegetation projects often deliver suboptimal outcomes due to the recolonization of invasive pasture grasses, but little is known about the effects of grass reinvasion on the survival and growth of established saplings. Even less is known about the costs and benefits of controlling pasture grasses once they have reinvaded.
2. To address these knowledge gaps, we implemented a split-plot grass control experiment in a 2-year old subtropical rainforest restoration planting in South East Queensland, Australia, that was reinvaded by the exotic pasture grass *Chloris gayana*.
3. Grass removal involved brush cutting around saplings, spraying herbicide and then laying 1 m² jute matting. The costs of implementing the treatment were recorded, and the survival, growth and physiological stress of treated and control saplings were monitored for 1 year.
4. Non-target herbicide application reduced survival by 6.5% in treated saplings, affecting mainly smaller plants that were below the grass canopy at the onset of the experiment. Beyond this direct herbicide effect, smaller treated saplings were also more stressed (lower chlorophyll fluorescence) and had substantially lower survival after 1 year than untreated saplings of the same size. There was limited evidence that removing grass increased growth rates, even for saplings that were already taller than the grass canopy at the start of the experiment.
5. While the growth benefits of controlling grass may become more apparent with time, our results suggest that grass removal is not an effective management strategy in untended plantings due to the heightened risk of sapling mortality, coupled with the considerable labour and material costs.

KEYWORDS

exotic grass, pasture, photoinhibition, plant traits, rainforest restoration, weed management

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1 | INTRODUCTION

Ecological restoration has become a valuable tool for reinstating habitat and ecosystem services in degraded landscapes (Bullock et al., 2011; Society for Ecological Restoration, 2019). In Australia, over two centuries of European land use has left a legacy of extensive ecosystem degradation, with more than 15% of the country's total land area either cleared or transformed (McAlpine et al., 2009). This history of land-use change has undoubtedly contributed to Australia's current biodiversity crisis by reducing, fragmenting and degrading the habitat of many plant and animal species (Bradshaw, 2012). In response, state and federal Governments have invested heavily in the restoration of degraded land as a strategy to prevent further biodiversity loss (Biodiversity Working Group, 2016).

The considerable scale of such investments, as well as Australia's daunting rates of species decline, accentuates the need for cost-effective, reliable and successful restoration projects. Restoration costs and outcomes can vary substantially depending on initial land condition, methods used, project size and maintenance requirements (Catterall & Harrison, 2006). The considerable expense of ecological restoration, especially that of tropical and sub-tropical rainforest, is frequently highlighted (Birch et al., 2010; Shoo & Catterall, 2013; Yeo & Fensham, 2014). Allocation of a limited budget is a significant challenge where funds are distributed amongst a range of competing projects, especially considering the uncertainty associated with restoring degraded systems (Shoo et al., 2017). Additionally, ecosystem recovery requires choosing between a variety of interventions, each possessing different costs, timeframes and probabilities of success (Wilson et al., 2011).

While passive strategies (i.e. natural regeneration) can be effective in some situations, their applicability in Australia's highly modified tropical and subtropical landscapes is limited due to the persistence of exotic grass and shrub species which impede passive ecosystem recovery (Kettenring & Adams, 2011; Shono et al., 2007; Shoo et al., 2017). As such, active revegetation approaches are widely implemented, and typically aim to achieve rapid canopy closure to shade out grass species and thus minimize ongoing maintenance costs (Goosem & Tucker, 1995; Kooyman, 1996; Neilan et al., 2006). However, complete progression from an exotic pasture to an intact, native system is often difficult to achieve. Where maintenance ceases prior to canopy closure, pasture grasses are likely to re-establish, reducing seedling growth and survival and potentially halting project progression (Reid et al., 2009).

Prior to canopy closure, planted individuals can experience strong competition from invasive species (Catterall & Harrison, 2006). It has been extensively reported that 'weed competition' during the establishment period leads to suboptimal restoration outcomes, with exotic species typically more efficient at utilizing resources over short timescales than native species (Funk & Vitousek, 2007). For example, the invasive grass *Avena barbata* depleted surface moisture and out-competed woody native species recolonizing abandoned farmland in

the Western Australian wheatbelt, with an increase in tree seedling establishment observed following grass removal (Standish et al., 2008). This may be attributed to the dense root systems of grasses in the upper soil layers, which efficiently usurp soil moisture and reduce its availability for woody species (Williams & Hobbs, 1989). Moreover, rapid nutrient acquisition by invasive grass has been shown to reduce nitrogen uptake by native species, leading to reduced annual biomass accrual (Mangla et al., 2011). Small seedlings may also experience strong light competition from rapidly recolonizing pasture grasses (Celis & Jose, 2011; Sun & Dickson, 1996). In Hawaii's submontane forest, removal of non-native perennial grasses increased light levels close to the soil surface, contributing to the increased growth of native woody shrub seedlings (D'Antonio et al., 1998).

The ability of exotic grasses to capitalize on increased resource availability often results in the formation of broadscale monocultures (Funk, 2008), which can lead to the smothering of neighbouring plants (Goosem & Tucker, 2013). In such instances, young seedlings and re-shooting plants may experience diminished growth and survival rates resulting, in part, from significant reductions in light availability (Celis & Jose, 2011; Sun & Dickson, 1996). For example in Hawaii's submontane forest, control of non-native perennial grasses increased light levels close to the soil surface and contributed to the increased growth of native woody shrub seedlings (D'Antonio et al., 1998). But the capacity of planted individuals to capitalize on the removal of grass is likely to vary substantially by species (Garcia-Serrano et al., 2007; Poorter, 2002). These species-level differences can be captured by measuring functional traits, defined as measurable attributes of plants that describe their physiological tolerances and ecological strategies (Cornelissen et al., 2003). Increasingly, plant traits are being used to predict the success of ecological restoration interventions and guide species selection in a variety of systems (Sandel et al., 2011).

Restoration success is a subjective and ambiguous descriptor of project outcomes, and a variety of attributes are used across restoration projects to characterize and evaluate progress (Wortley et al., 2013). In the context of active restoration, it is generally accepted that high rates of seedling establishment and low rates of weed reinvasion are reliable measures of success, and projects that do not deliver these outcomes are widely perceived as failures (Suding, 2011). But compared to the expense and uncertainty associated with starting new projects, intervening in existing projects that have delivered suboptimal outcomes (e.g. due to weed reinvasion) may prove cost-effective.

This study focuses on an existing restoration project located at Oxley Creek Common (South East Queensland, Australia) that aimed to transform grazed pasture to riparian rainforest along 1.5 km of alluvial floodplain. A field experiment was embedded in this project comprising plots planted with functionally different species mixes to examine the trade-off between growth rate and stress tolerance. Unfavourable weather conditions during the planting and establishment period resulted in low initial survival rates. These conditions, combined with minimal site maintenance, led to widespread

recolonization by various exotic species, particularly Rhodes grass (*Chloris gayana*). While not intended at the onset of the project, grass recolonization presented an opportunity to assess the impacts of exotic pasture grass control on sapling performance. Such information is crucial given how widespread the issue of grass competition is in forest restoration in Australia (Hagger et al., 2017) and elsewhere (Guariguata et al., 1995).

Specifically, through the implementation of a manipulative field experiment, we address the following questions:

1. How does the removal and suppression of exotic grass affect the survival and growth of established rainforest tree saplings?
2. Do measures of plant stress (chlorophyll fluorescence) align with the survival and growth data?
3. Relative to the costs of implementation, what were the ecological costs and benefits of the treatment?

2 | MATERIALS AND METHODS

2.1 | Study site

Located on an alluvial floodplain in one of Brisbane's southern suburbs, Oxley Creek Common (27°32'S 152°59'E) was cleared entirely for agriculture in the early 20th century. The site is adjacent to Oxley Creek, one of the Brisbane River's major tributaries, and now contains pasture and small patches of freshwater wetland that are prone to inundation. The floodplain comprises dermosols with remnants of sandy alluvium (Beckmann et al., 1987). Prior to clearing, a variety of regional ecosystems (REs) are likely to have been present, with complex notophyll to microphyll vine forest (RE 12.3.16), *Eucalyptus* open forest (RE 12.3.11) and *Melaleuca* open forest (RE 12.3.5) the most expansive vegetation communities (Queensland Government, 2019).

In November 2016, the Oxley Creek Catchment Association, in partnership with researchers at The University of Queensland, established a project to restore a corridor of lowland riparian rainforest. Funded by the Australian Government's '20 Million Trees' programme, the project incorporated an experiment investigating two distinct species mixes ('Fast' and 'Hardy'). Tree species were selected using a trait-based target approach (Gardiner et al., 2019; Laughlin, 2014); the 'Fast' mix contained species with traits reflecting high resource acquisition, whereas the 'Hardy' mix included species with traits reflecting more conservative strategies. Twenty-four species were selected (Table S1 in the Supporting Information), with 'Fast' and 'Hardy' mixes each possessing eight unique species and sharing eight species with intermediate trait profiles. Ten blocks, each containing two plots, were distributed along Oxley Creek using a randomized block design, with a 'Fast' or 'Hardy' mix randomly assigned to each plot pair (Figure S1 in the Supporting Information in the Supporting Information). Each plot was 30 × 30 m, containing 400 seedlings planted with 1.5 m spacing. Only the first 12 plots were assessed in this study.

2.2 | Existing functional trait data

Functional trait data were sourced for all 24 study species from earlier research at the study site (Gardiner et al., 2019). Traits included specific leaf area (SLA), leaf dry matter content, lamina area, leaf type (simple or compound), wood density, root tissue density and specific root length. Leaf type, square-root-transformed lamina area and log-transformed SLA were largely orthogonal, and thus suitable for inclusion in the following statistical models.

2.3 | Split-plot weed control experiment

The previous investigation at this site (Gardiner et al., 2019) focused on survival and growth of planted seedlings during the establishment period (i.e. seedlings were monitored in February 2017, 3.5 months after planting). After this period, the plots received minimal follow-up maintenance and were recolonized by a variety of exotic pasture species, predominantly *Chloris gayana*, over the subsequent 2 years. In February 2019, the survival and height of all saplings in plots 1–12 were recorded to provide baseline data for the current experiment. Only plots 1–12 were selected for this study due to the colonization of large, woody weeds (e.g. *Schinus terebinthifolius*) in plots 13–20. The split-plot experiment was implemented in May 2019 and involved controlling grass and exotic forbs around the surviving saplings in one half of each plot. Plot halves were selected to minimize differences in the number and composition of surviving saplings (Table S1). The treatment was implemented in conjunction with experienced restoration practitioners. Firstly, 'spotters' used plot maps to identify surviving plants, which were then marked clearly by hand-removing all grass within 30 cm of each sapling. The grass which remained within 1 m² of each sapling was then slashed using a brush-cutter, with particular care taken not to damage the focal plant. A herbicide solution containing Roundup (10 mL glyphosate per litre of water), Starane (3 mL/L fluroxypyr) and a pink Envirodye (2 mL/L) was then applied to the foliage of remaining grasses and forbs in the cleared area to prevent regrowth. Starane was used in combination with Roundup to ensure that small, woody weeds such as *Sida cordifolia* were also targeted. In order to minimize herbicide drift and maximize absorption, herbicide was only applied on days where neither rain nor strong winds were forecasted. One week after the herbicide application, all treated saplings were monitored to assess death or damage caused by spray drift. Symptoms included mottled chlorosis, leaf necrosis and plant dieback (Feucht, 1988). All saplings that showed symptoms subsequently died, allowing us to confidently quantify herbicide-related mortality. After waiting 2 weeks to maximize the impact of herbicide application, jute matting (1 × 1 m) was installed around the base of each sapling (Figure S3 in the Supporting Information). The 1 m² area to be matted was cleared of dead vegetation, and the mat was secured using five 200 mm pegs. Detailed records of labour and materials costs were collected to assess cost-effectiveness (Table 1). Upon remeasuring sapling heights (May 2020), it was noted that the treatment had been effective in

TABLE 1 Expenses associated with the grass removal treatment

Item	Unit cost	Total cost (AUD)
Paid labour (146 h)	\$55/h	\$8,250
Volunteer labour (80 h)	\$0/h	\$0
Starane (1.05 L)	\$24.5/L	\$25.73
Glyphosate (3.5 L)	\$9.95/L	\$34.83
Envirodye (350 mL)	\$34/L	\$11.90
Jute matting (813 m ²)	\$3/m ²	\$2,439
Pegs (4,065)	\$0.21/peg	\$853.65
		\$11,395.11

restricting grass growth around each sapling, with only herbaceous weeds (e.g. *Cirsium vulgare*) having penetrated the jute matting.

2.3.1 | Chlorophyll fluorescence

Chlorophyll fluorescence (F_v/F_m) was measured using a handy PEA chlorophyll fluorimeter (Hansatech Instruments Ltd, King's Lynn) on a subset of saplings in August 2019 to provide an indication of physiological stress. To determine species-specific dark adaptation durations, measurements were taken at 5-min intervals on a single sample until the F_v/F_m value did not increase any further. Leaf clips were used to cover the sample area, and the shutter plate was opened after the specified duration, once the fluorimeter was attached. Samples were measured for 1 s at maximum light intensity ($3500 \mu\text{mol m}^{-2} \text{s}^{-1}$). This generated a species-specific dark adaptation duration.

Measurements were taken in plots 1, 2, 5, 6, 11 and 12 to span environmental variation (Figure S1). Measurements were performed on 12 species from across the measured functional trait space (Table S1). Individuals of each species were sampled in both untreated and treated plot halves; however, the total number of sampled individuals per species varied depending on the number of surviving saplings. An equal number of individuals were sampled in 'Hardy' and 'Fast' plots and treated and untreated plot halves, with 200 saplings sampled overall. In each plot, individuals of each species were randomly selected to ensure that within-plot spatial variation and a range of heights were captured. For each individual, F_v/F_m was measured using a randomly selected leaf that was mature but not senescing.

2.3.2 | Soil moisture

Volumetric water content was measured using a FieldScout TDR 100 soil moisture meter (Spectrum Technologies Inc, Chicago, USA), with two 20 cm probes. Within each plot, 10 saplings were randomly selected in both the treatment and control plot halves to ensure that within-plot spatial variation was adequately captured. Measurements at each sapling location were made in triplicate, within 30 cm of the base of each plant, and dense leaf litter was removed prior to insert-

ing the probes. All measurements were made on 6 July 2019, 10 days after 16 mm rain at the study site.

2.4 | Statistical analyses

All statistical analyses were conducted in R Version 3.6.3 (R Core Team, 2019) via RStudio Version 1.2.5033 (RStudio Team, 2019). We fitted hierarchical Bayesian models in Stan (Carpenter et al., 2017), using the brm function in the brms package (Bürkner, 2017). In all cases we adopted the default, weakly informative prior distributions for regression coefficients and variance parameters. Four Markov chains were used with a minimum of 2000 iterations including a 1000 iteration warm-up. Model convergence was assessed visually and via the Rhat statistic (Gelman & Rubin, 1992). Our models with weakly informative prior distributions are analogous to (generalized) linear mixed-effects models fitted using frequentist methods. We prefer Bayesian inference because it allows for more flexible model fitting and generates posterior distributions for all model parameters. We also calculated the 'probability of direction' (pd; Makowski et al., 2019a) for all fixed-effect estimates using the p_direction function in the bayestestR package (Makowski et al., 2019b). As the name suggests, pd is the probability that an effect exists in a particular direction (ranging from 0.5 to 1) and is therefore conceptually related to frequentist p -values. In fact pd values of > 0.975 are analogous to two-tailed p -values of < 0.05 , though we do not report p -values here.

2.4.1 | Non-target sapling mortality

Mortality associated with non-target herbicide application was modelled using a binary variable (spray symptoms = 1, no spray symptoms = 0), excluding individuals located in control plot halves that were not sprayed ($n = 795$). This response was modelled as a function of initial plant height (in February 2019) using a Bernoulli error distribution and logit link function. Random intercepts were included to reflect the nesting of observations spatially (saplings within plots, within blocks). We also fitted species-level regressions as random effects which included log-transformed initial plant height.

2.4.2 | Subsequent sapling performance

Saplings that died from non-target herbicide application were removed from further analyses. The performance of remaining saplings was then examined in three models: probability of survival ($n = 1565$), probability of positive growth ($n = 1394$) and height growth ($n = 1206$). The 'probability of positive growth' model was required because many saplings survived but experienced no height growth or even lost height. Thus, this model included all surviving saplings and had a binary response indicating those that gained height (1) and those that did not (0). For saplings that gained height, their height growth rate was calculated as $(\text{Height}_{t_{1i}} - \text{Height}_{t_{0i}}) / (t_{1i} - t_{0i})$, where t_{0i} was the date that sapling i was measured during February 2019 and t_{1i} is the date that sapling i was remeasured during May 2020.

Binary survival and positive growth response variables were modelled using a Bernoulli error distribution and logit link function. The height growth rate was square-root-transformed to approximate a normal distribution and modelled using a Gaussian error distribution and identity link function.

All three models had the same fixed and random effects. Fixed effects included treatment (control or grass removal), log-transformed initial plant height, log-transformed SLA, sqrt-transformed lamina area and leaf type (simple or compound), as well as two-way interactions between treatment and each of the other variables. Explanatory variables were standardized (mean = 0, SD = 1) to enable comparison of model coefficients. Random intercepts were included in all models to reflect the nesting of observations spatially (saplings within plots, within blocks). We also fitted species-level regressions as random effects which included treatment, log-transformed initial plant height and their interaction. This permitted each species to vary in the size-dependent response to the control and grass removal treatments. By default, the brm function also estimates the necessary correlation parameters for each combination of these species-level random effects.

2.4.3 | F_v/F_m

F_v/F_m measurements were logit-transformed and modelled using a Gaussian error distribution and identity link function ($n = 204$). Fixed effects included the treatment, which was allowed to interact with log-transformed plant height. Spatial and species random effects were included as in all other models.

2.4.4 | Experimental effects on soil moisture content

Volumetric water content measurements (proportions) were also logit-transformed and modelled using a Gaussian error distribution and identity link function ($n = 240$). One random effect was included to account for the spatial nesting of plants within plots. Treatment was the sole fixed effect to test for an overall difference in soil moisture content between treatment and control plot halves.

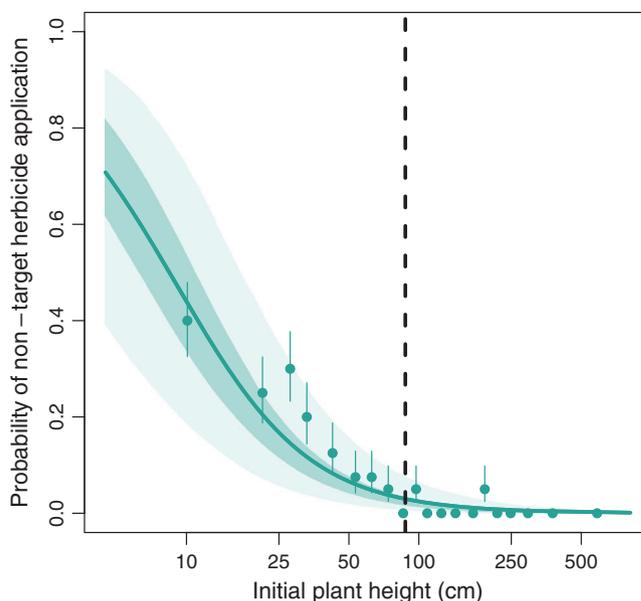


FIGURE 1 Fitted relationship between initial sapling height (February 2019) and the probability of non-target herbicide application. Only treated individuals were included in the model. Envelopes around each line are 95% credible intervals (most translucent) and 50% credible intervals (least translucent) calculated using only fixed effects (i.e. they are population-level credible intervals). To provide an indication of how the binary survival data correspond to each fitted relationship, we first ordered the binary response according to initial plant height. We then divided this ordered binary variable into 20 bins of increasing plant height and calculated the mean probability (points) and associated standard error (bars) for each bin. The black, dashed line represents the mean grass height surrounding saplings (87 cm) prior to implementation of the experiment

3 | RESULTS

3.1 | Herbicide application

Non-target herbicide application resulted in the death of 6.5% of treated saplings. The probability of being accidentally sprayed with herbicide was negatively related to sapling height ($pd = 1$, indicating high probability that this effect is negative). Individuals below 20 cm had a spray probability greater than 0.2 (Figure 1). For individuals taller than the mean grass height (87 cm), the probability of accidentally being sprayed with herbicide was less than 0.05.

3.2 | Survival (excluding saplings killed by non-target spraying)

The grass control treatment reduced sapling survival ($pd = 1$; Table S2 in the Supporting Information); the overall survival probability in control and treatment groups was 0.96 and 0.80, respectively. Initial height interacted with treatment such that small, treated saplings (< 100 cm) were far less likely to survive the experimental period compared to

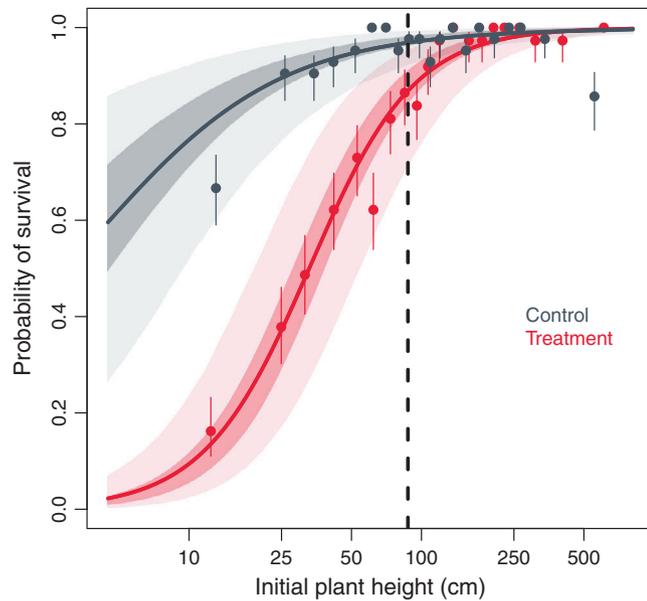


FIGURE 2 Fitted relationships between the probability of survival and initial plant height (February 2019), with separate lines fitted for the grass removal treatment and control groups. All other variables in the model (e.g. trait variables) were held at their mean when plotting these relationships. Envelopes around each line are 95% credible intervals (most translucent) and 50% credible intervals (least translucent) calculated using only fixed effects (i.e. they are population-level credible intervals). Points and standard error bars were calculated for each treatment as described in Figure 1. The black, dashed line represents the mean grass height surrounding saplings (87 cm) prior to implementation of the experiment

control saplings (Figure 2; $pd = 0.999$; Table S2). The effect of SLA on survival was negative for control plants (main SLA term; $pd = 0.979$) but weak compared to the effects of treatment and initial plant size. On the probability scale, this effect was negligible because of the very high survival of control plants. For treated saplings, the SLA effect remained negative such that the lowest SLA species ($6 \text{ mm}^2 \text{ mg}^{-1}$) had an estimated survival probability of > 0.95 , whereas the highest SLA species ($35 \text{ mm}^2 \text{ mg}^{-1}$) had an estimated survival probability < 0.8 (plot not shown). For all other coefficients involving traits the effects sizes were small and pd values were < 0.965 (Table S2).

3.3 | Probability of positive growth

The grass control treatment also reduced the probability of positive growth ($pd = 0.999$; Table S3 in the Supporting Information); the overall probability of positive growth was 0.92 and 0.82 for control and treatment saplings respectively. Similar to the survival model, initial height interacted with treatment such that small, treated saplings were less likely than control saplings to achieve positive growth (Figure 3; $pd = 0.984$; Table S3). Again, the effect of SLA was negative for control and treatment plants (plot not shown), but these effects were weaker than in the survival model and were associated with moderate pd values ($pd < 0.96$ for main and interaction terms for SLA). The effect sizes were small, and pd values were < 0.8 for the remaining trait terms.

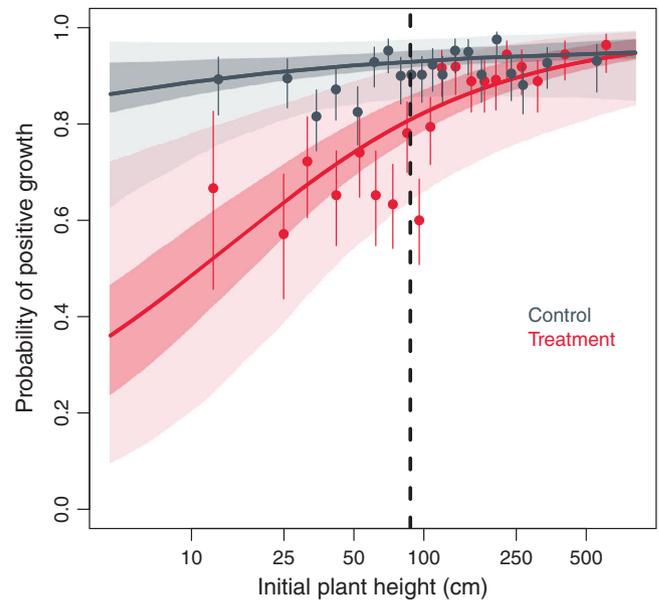


FIGURE 3 Fitted relationships between the probability of positive growth and initial plant height (February 2019), with separate lines fitted for the grass removal treatment and control groups. All other variables in the model (e.g. trait variables) were held at their mean when plotting these relationships. Envelopes around each line are 95% credible intervals (most translucent) and 50% credible intervals (least translucent) calculated using only fixed effects (i.e. they are population-level credible intervals). Points and standard error bars were calculated for each treatment as described in Figure 1. The black, dashed line represents the mean grass height surrounding saplings (87 cm) prior to implementation of the experiment

3.4 | Height growth rates (of saplings that experienced positive growth)

The effect of grass removal on height growth was extremely weak and highly uncertain (Table S4 in the Supporting Information; $pd = 0.725$). Overall, control and treatment saplings displayed average growth rates of $0.088 \text{ cm day}^{-1}$ and $0.091 \text{ cm day}^{-1}$, respectively, which equates to mean total height growth of 36.3 and 37.6 cm over the experimental period. Unlike the models for survival and positive growth, the interaction between initial height and treatment was weak and uncertain (Figure 4; Table S4; $pd = 0.840$). Effects sizes were also very small and for all terms involving traits (Table S4).

3.5 | F_v/F_m and soil moisture

The interaction between treatment and plant height in the F_v/F_m model was strong and highly certain (Table S5 in the Supporting Information; $pd = 0.999$). This interaction indicated that saplings $< 120 \text{ cm}$ were more stressed in the treatment compared to the control (Figure 5). Larger treated saplings ($> 210 \text{ cm}$) appeared less stressed than control saplings (Figure 5), at least at the time of measurement which was 4 months after implementation of the experiment. The grass removal treatment had a small positive effect on soil moisture beneath saplings

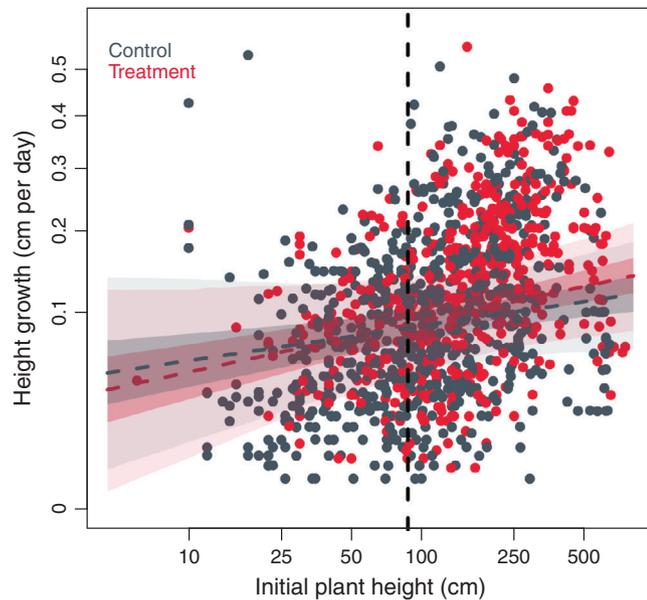


FIGURE 4 Fitted relationships between sqrt-transformed plant height growth (cm per day) and initial plant height (February 2019), with separate lines fitted for the treatment and control groups. The pd value for the treatment:log(initial plant height) interaction term was only 0.84 indicating a low probability that the effect existed. All other variables in the model were held at their mean when plotting these relationships. Envelopes around each line are 95% credible intervals (most translucent) and 50% credible intervals (least translucent) calculated using only fixed effects (i.e. they are population-level credible intervals). The black, dashed line represents the mean grass height surrounding saplings (87 cm) prior to implementation of the experiment

(treatment coefficient in logits = 0.13; pd = 0.998). This equated to a 3% difference in soil moisture between control and treated saplings.

3.6 | Costs

With a team of five people, brush-cutting and herbicide application was completed in 14 h. The jute mats were laid by four experienced bush regenerators (19 h each) and 20 volunteers who each contributed 4 h. In total, the treatment required 226 h of labour and cost \$11,395 AUD (Table 1). On average, with a team of five people, it would have required 3.4 min and \$14.40 to treat each sapling.

4 | DISCUSSION

Due to the inherent risks associated with active ecological restoration, and the expense it incurs, critical evaluation of empirical data is required to identify barriers to successful restoration and improve future outcomes. In particular, with the pervasive threat of invasive plant species, outcomes are often compromised by a lack of cost-effective weed management strategies (Hagger et al., 2017). While many studies have explored the impact of weed control on initial seedling establishment, few have returned to reinvaded sites to inves-

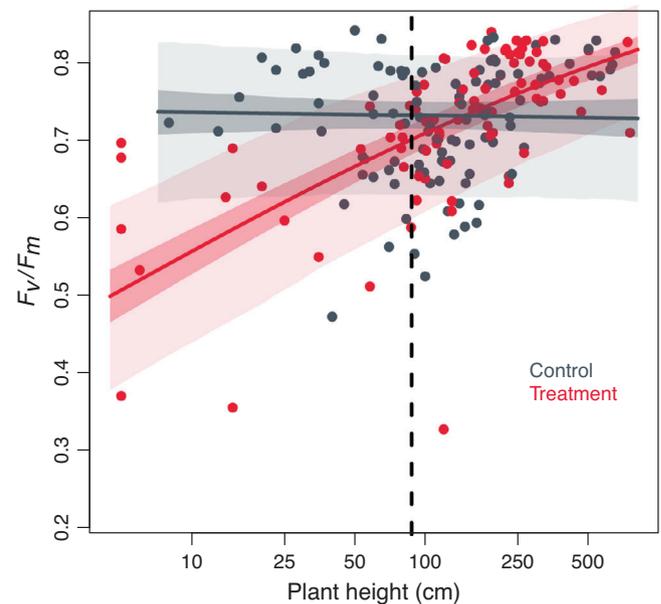


FIGURE 5 Fitted relationships between chlorophyll fluorescence (F_v/F_m) and log-transformed plant height, with separate lines fitted for the treatment and control groups. Envelopes around each line are 95% credible intervals (most translucent) and 50% credible intervals (least translucent) calculated using only fixed effects (i.e. they are population-level credible intervals). The black, dashed line represents the mean grass height surrounding saplings (87 cm) prior to implementation of the experiment

tigate the effects of interventional management practices on plant growth and survival. This study utilized an existing restoration project showing suboptimal outcomes to test the effectiveness of a weed treatment for improving growth and survival of tree saplings. Not only did grass removal prove costly, it also reduced the survival of smaller saplings compared to those in the control and had negligible effects on growth. In addition, the measured functional traits did not explain species-level differences in their responses to grass removal, suggesting the responses to grass removal were quite general across sapling trait space.

4.1 | Sapling growth and survival

The grass control treatment substantially reduced sapling survival, with small, treated saplings exhibiting the lowest survival probability. The survival probability of treated saplings increased sharply with height, plateauing at approximately 100 cm (Figure 2). Additionally, treated individuals less than 110 cm were less likely to display positive growth compared to saplings in the control (Figure 3). Given that the mean height of grass was 87 cm, it is possible that the removal of grass caused physiological stress associated with sudden exposure. Frost damage is unlikely to have contributed to this response, as during the experimental period, temperatures did not drop below 4°C near the study site (Bureau of Meteorology, 2019).

Mortality and reduced growth in response to increased exposure to high irradiance has been observed in other manipulative studies,

resulting either from grass removal (Zimmerman et al., 2001) or canopy opening (Brown & Whitmore, 1992). Accordingly, it is likely that the reduction in plant performance observed in this study was associated with light intensity, whereby saplings became photoinhibited due to high levels of irradiance (Holl, 1999; Loik & Holl, 2001). Photoinhibition is characterized by a decrease in photosynthetic efficiency resulting from damage to the photosynthetic apparatus, which occurs when ambient light levels surpass an individual's capacity for energy processing (Osmond, 1994). This response is observed in natural settings upon the transition of shade-grown plants to direct sunlight in canopy gaps and is reported in studies as an abrupt decline in the chlorophyll fluorescence measurement, F_v/F_m (Lovelock et al., 1994). While chlorophyll fluorescence was not measured prior to implementing the treatment, lower F_v/F_m values were associated with treated saplings, particularly those below 100 cm in height (Figure 5) which had previously developed shade-leaves under a low-light grass canopy.

Although photoinhibition alone may seldom cause sapling death, it is likely to exacerbate prevailing environmental stressors (Langenheim et al., 1984). Given the reduced capacity for small saplings with limited root mass to extract water from drying soil, photoinhibitory stress may have interacted with low water availability during the winter dry period to limit both survival and daily height growth (Bjorkman & Powles, 1984; Luis & Alves, 2002). This is certainly a possibility considering that, during the experimental period, the study site received 49% less rainfall than the 90-year average (Bureau of Meteorology, 2019). Moreover, the abrupt exposure to wind upon the removal of grass may have caused desiccation, exacerbating moisture stress in small, treated individuals (Fajardo & McIntire, 2010).

F_v/F_m , measured 5 months during the experiment, indicated that smaller treated saplings (those initially under the grass canopy) were most stressed, and indeed these smaller treated saplings suffered the lowest survival by the end of the experiment (Figure 2). F_v/F_m data also suggested that taller treated saplings (those initially above the grass canopy) may benefit from pasture grass removal, as these taller individuals had higher F_v/F_m values compared to equivalent plants in the control (Figure 5). While larger saplings experienced similarly high survival to control saplings by the end of the experiment, the apparent benefit of grass removal evident in medium-term F_v/F_m values did not translate to a detectable growth benefit by the end of the experiment. However, the direction of the weak interaction between initial height and treatment (Figure 4) in the height growth model was at least consistent with the F_v/F_m data (Figure 5).

Increased plant performance following grass removal is often attributed to an increase in soil water availability (Ammond et al., 2012). The use of jute matting and grass removal in this study increased soil moisture under treated saplings by around 3% on average. Due to the dense root mass of pasture grasses concentrated in the surface layer of soils, other studies have revealed that the removal of grass alone significantly increased soil moisture availability (Thaxton et al., 2012; Nepstad et al., 1996). However, it is important to note that soil moisture measurements in this study were taken 10 days after heavy rainfall and as such, is unlikely to be representative of water availability during prolonged periods without precipitation. Indeed, the low rainfall

experienced at this site, particularly following grass removal, may have suppressed potential survival and growth benefits of treated saplings.

4.2 | Costs, benefits and implications

It is beyond the scope of this study to undertake a detailed, cost-benefit analysis for the grass control treatment; in part, because the duration of the experiment was too short to estimate the full growth benefits. It is likely that grass was slowing the growth rate of small saplings prior to the experiment – this is consistent with our observations and the findings of other studies (Holl, 1998). As such, we predicted that reducing grass competition would have had a positive effect on the growth rate of smaller, suppressed saplings; however, the experiment did not reflect this. Treated saplings were more prone to non-target herbicide application, had lower subsequent survival probabilities and were less likely to display positive growth. Furthermore, greater treatment costs were associated with small saplings, as they took longer to find, and additional personnel (spotters) were required to locate these individuals. As such, we found limited support for interventional grass removal, even for saplings that were already taller than the grass canopy at the start of the experiment.

Based on the results to date, it is recommended that the removal of grass followed by jute matting is not a cost-effective weed management strategy; rather, it incurs a multitude of plant performance costs and delivers no clear benefits in the first year. Given this result, it may be worth investigating the effectiveness of less direct forms of exotic grass control such as shading structures (Thaxton et al., 2012). Weed control strategies should be sought that are less likely to result in immediate reductions in plant survival, as experienced by treated saplings in this study through non-target herbicide application and photoinhibitory stress. Furthermore, it was expected that the capacity of saplings to persist in dense grass (i.e. the control treatment) until adjacent trees shade out the grass, would be dependent on species-level functional traits. However, there was limited evidence to support trait-modulated treatment responses in our survival model (Table S2), or any other model for that matter. It may be that plastic trait responses to shading are more informative than species average trait values in this context – a topic worthy of future research.

Ecological restoration is crucial for ensuring biodiversity persistence and human wellbeing in light of ongoing environmental degradation (Perring et al., 2015). However, restoration projects commonly deliver suboptimal outcomes, such as the reinvasion of exotic pasture grasses. Consequently, research regarding the cost-effectiveness of intervening in existing projects, as a means of salvaging better outcomes, is urgently required. This study supports the need for such research, revealing unexpected yet compelling results that can be used to shape future management strategies.

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AUTHORS' CONTRIBUTIONS

J.M.D. and L.S. conceived the idea. J.R.S. implemented the experiment and collected and processed the experimental data with input from J.M.D. Statistical analyses were performed by J.R.S. and J.M.D. The manuscript was written by J.R.S. with support from J.M.D.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.c2fqz617m> (Radford-Smith & Dwyer, 2021).

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