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Author/s:

Moser, S;Greet, J

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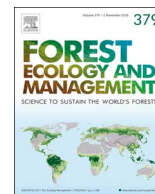
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Unpalatable neighbours reduce browsing on woody seedlings

Sarah Moser*, Joe Greet

School of Ecosystem and Forest Sciences, The University of Melbourne, 500 Yarra Boulevard, Richmond, Victoria 3121, Australia



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ABSTRACT

High levels of browsing by mammalian herbivores can negatively affect the survival and growth of seedlings, and consequently revegetation and forest regeneration outcomes. Typical forms of protection (e.g. tree guards and fencing) are costly, particularly when used in large-scale projects, therefore, low-cost alternatives are needed. Based on associational refuge theory, we assessed the revegetation technique ‘cryptic planting’, whereby woody seedlings are planted within the foliage of unpalatable plants to deter browsing. We established a trial where 432 six-month-old tubestock of three woody species (*Eucalyptus camphora*, *Melaleuca squarrosa* and *Leptospermum lanigerum*) were cryptically (within the foliage perimeter of unpalatable plants) or non-cryptically planted across three wetland forest sites. The plants were left for four weeks before being scored for browsing damage based on an estimate of biomass removed. To further assess cryptic planting, we surveyed 352 plants of the same three woody species two years after they were planted cryptically or non-cryptically at the same three sites, and surveyed each plant for browsing damage. Overall, cryptic planting reduced browsing damage from 37% to 22%, and from 51% to 23%, in the trial and survey, respectively. *E. camphora* plants were particularly susceptible to browsing. These results suggest that cryptic planting provides an alternative to costly tree guards and fencing and can be used to reduce browsing on woody seedlings.

1. Introduction

High levels of mammalian browsing are known to reduce the survival and growth of seedlings (Bulinski and McArthur, 1999; Horner et al., 2016). Consequently, severe browsing can negatively impact on revegetation projects by hampering restoration outcomes and reducing regeneration growth rates (Wilkinson and Neilsen, 1995). Current forms of control measures are costly (e.g. tree guards and fencing) particularly when used in large-scale projects, therefore, effective low-cost alternatives are needed.

Various control measures are used worldwide to reduce the impacts of browsers on seedlings. For example, tree guards are known to reduce browsing damage to seedlings by providing protection in the early years of growth (Kasel, 2008; Alexander et al., 2016). However, high economic costs are associated with the installation, post-planting maintenance and eventual removal of the tree guards. Similarly, while enclosures can be used to keep browsers out of areas targeted for revegetation, the installation and maintenance of fences is also costly. Lethal control is another method used to manage high populations of browsers, but ethical and safety concerns from the community may arise from such approaches, particularly when controlling populations of native browsers (Baker et al., 2007).

An alternative approach is to use plant-herbivore interactions and

the traits of the surrounding vegetation to reduce browsing damage. Associational refuge theory (Pfister and Hay, 1988) suggests that unpalatable neighbouring plants can provide protection to a focal plant from browsers, thereby reducing browsing. Protection may come in the form of physical structures like thorns and spines (Hanley et al., 2007), or chemical characteristics such as toxins that influence palatability. Similar to indirect interactions whereby one species lessens the effect of another species on a third species (Sotomayor and Lortie, 2015), associational refuge also shares similarities to the concepts of facilitation and nurse plants, where one plant indirectly improves conditions for another plant (Callaway, 1995; Mandujano et al., 1998).

In south-east Australia, associational refuge is being used in wetland restoration through the planting method of ‘cryptic planting’, whereby seedlings are planted within the foliage perimeter of unpalatable plants to reduce post-planting mammalian browsing (Raulings et al., 2014). The term ‘cryptic planting’ is not evident in the literature, instead it appears to be primarily used among land managers. Nonetheless, the concepts of associational refuge and nurse plants have been used to minimise herbivory in the restoration of woodlands (Smit and Ruifrok, 2011; Stutz et al., 2015), wooded pastures (Smit et al., 2005), and in forest plantations (Miller et al., 2006). However, little is known of its efficacy to deter browsing in wetland areas.

For this study, we assessed cryptic plantings in wetland forests in

* Corresponding author.

E-mail address: sarah.moser@unimelb.edu.au (S. Moser).

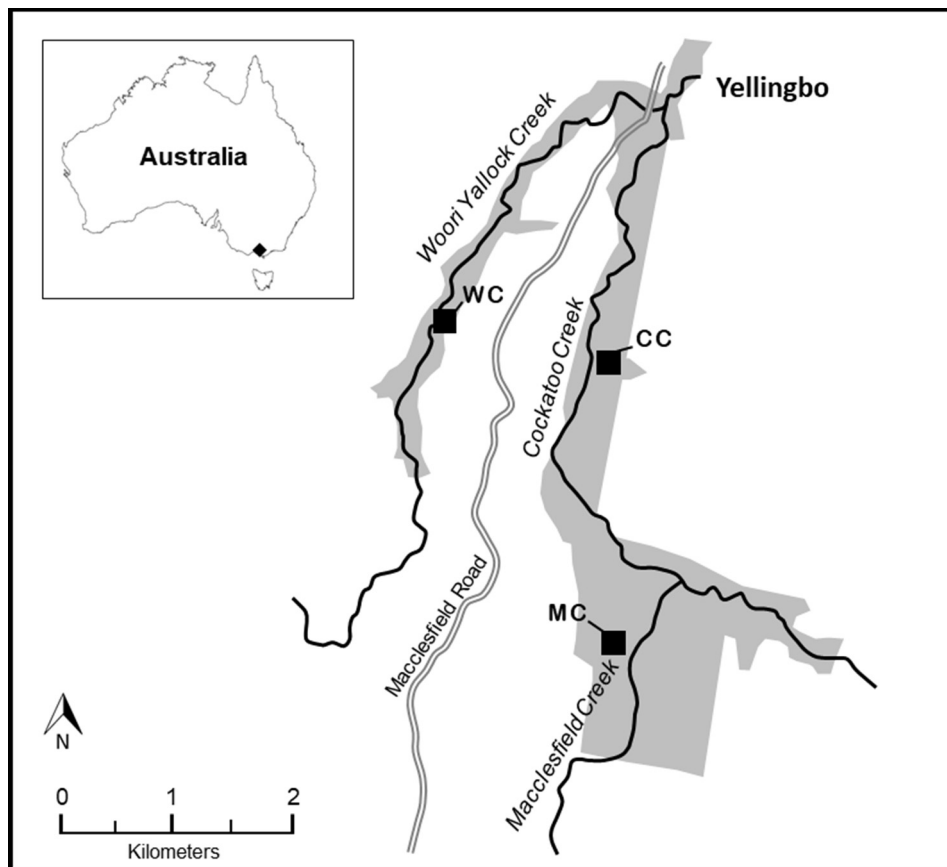


Fig. 1. Map of Yellingbo NCR with study sites denoted by black squares (WC: Woori Yallock Creek; CC: Cockatoo Creek; MC: Macclesfield Creek). Grey shading shows the extent of the reserve, black lines indicate streams, double lines indicate roads. The insert shows the location of reserve (black filled diamond) in relation to Australia.

the Yellingbo Nature Conservation Reserve (Victoria, Australia). Our research aimed to assess whether cryptic planting could be used as an effective tool for minimising browsing damage to planted woody seedlings. Using both field trial and survey methods, we assessed whether cryptic planting within sedges reduced browsing damage to planted seedlings of three woody species.

2. Material and methods

2.1. Study area

Our study was conducted at three wetland forest sites located within the Yellingbo Nature Conservation Reserve (NCR), located approximately 50 km east of Melbourne (Victoria, Australia) (Fig. 1). The reserve covers an area of ~640 ha and is surrounded by cleared agricultural land. It contains the largest extent of the ‘Sedge-rich *Eucalyptus camphora* (mountain swamp gum) Swamp Community’, which is listed as threatened under the Victorian *Flora and Fauna Guarantee Act (1998)* (Turner, 2003). This vegetation community provides habitat for the critically endangered Leadbeater’s possum (*Gymnobelideus leadbeateri*) and helmeted honeyeater (*Lichenostomus melanops cassidix*) that occur in the reserve (Blackney and Menkhorst, 1993; Harley et al., 2005).

This reserve has been the target of extensive revegetation since the late 1970s due to declining vegetation condition (Gadsen and Ashby, 1995). In the absence of costly tree guarding or fencing, revegetation efforts within the reserve are often severely hampered by browsing damage from herbivores. These include the native swamp wallaby (*Wallabia bicolor*), a medium-sized macropod that mainly feeds on forbs and shrubs, the introduced fallow deer (*Dama dama*), a medium-sized deer that mainly grazes but has been observed browsing on planted seedlings in the reserve, and the introduced sambar deer (*Rusa*

unicolor), a large deer that both grazes and browses (Davis et al., 2008; Forsyth and Davis, 2011). The eastern grey kangaroo (*Macropus giganteus*) and European rabbit (*Oryctolagus cuniculus*) are also present but are less likely to browse on woody plant seedlings due to habitat and dietary preferences (Davis et al., 2008).

We selected three riparian sites for this study located adjacent to three creeks that flow through the reserve: Cockatoo Creek, Macclesfield Creek and Woori Yallock Creek (Fig. 1.). The sites cover an area of 1.5 ha, 3.5 ha, and 2.3 ha respectively and consist of wet forests dominated by *E. camphora* on swampy sites and *E. viminialis* (manna gum) on more elevated sites, in association with shrub thickets dominated by either *Melaleuca squarrosa* (scented paperbark) or *Leptospermum lanigerum* (woolly tea tree). The understorey of these forests supports a diversity of large sedge species, including *Carex* spp., *Gahnia sieberiana* and *Lepidosperma laterale*.

Due to the low natural recruitment of woody species within the reserve, Greening Australia (a not-for-profit conservation organisation) revegetated the study sites from September–December 2014 as part of a national government-funded Landcare program, the Two Million Trees Project. The project involved planting 286,500 trees and shrubs within the reserve (Raulings et al., 2014). Due to funding constraints, plants were not guarded, however, cryptic planting was used where possible. Prior to planting, seedlings were also sprayed in the nursery with the browsing deterrent Sen-Tree™, an egg-based, acrylic polymer adhesive mixed with silicon carbide grit. Although the texture and odour of the product are thought to deter browsers, it has been found to be only effective in the short-term because the product does not protect new foliage growth (Miller et al., 2011).

2.2. Study species

The three woody plant species were selected for this study: *Eucalyptus camphora* subsp. *humeana* L.A.S. Johnson & K.D. Hill (mountain swamp gum), *Melaleuca squarrosa* Donn. ex. Sm. (scented paperbark), and *Leptospermum lanigerum* (Aiton) Sm. (woolly tea-tree). These species were selected as they were planted in high numbers (> 10,000 plants) at each study site, and form key habitat components for the critically endangered faunal species within the reserve (Pearce and Minchin, 2001; Harley et al., 2005).

Eucalyptus spp. and *Leptospermum* spp. are known to occur in the diet of the swamp wallaby (Hollis et al., 1986; Di Stefano, 2005; Stutz et al., 2015) and the two non-native deer species (Parker, 2009; Forsyth and Davis, 2011) present within the reserve, however the palatability of *Melaleuca* spp. is unknown.

The understorey species used for cryptic planting in this study included sedges *Carex appressa* R.Br., *Gahnia sieberiana* Kunth and *Lepidosperma laterale* R.Br. These species are characterised by sharp-edged leaves. At each study site, extant patches of these species were selected that were > 1 m in height and width.

2.3. Cryptic planting trial

To assess the effect of cryptic planting on browsing damage, we established a trial in early September 2016 using the three study sites. To ensure local provenance, the tubestock used were all grown from seed collected within the reserve, and grown by a local nursery (Friends of the Helmeted Honeyeater Nursery, Yellingbo). At the time of the trial, the tubestock were approximately six months of age and ~40 cm in height.

We used a randomised block design, consisting of three sites (WC, CC and MC; Fig. 1) with six blocks located at each of the three sites. In each block, we established a pair of patches 1–5 m apart, which comprised cryptic planting and non-cryptic planting treatments. The cryptic planting treatment comprised planting four tubestock each of *E. camphora*, *L. lanigerum*, *M. squarrosa* within the perimeter of an established patch of sedges (> 1 m × > 1 m), using a Hamilton tree planter. The four replicate plants of each species were planted in this manner with a minimum distance of 30 cm between plants. In contrast, the non-cryptic planting treatment consisted of tubestock of each species being planted in an exposed area (e.g. areas absent of large sedges). Again, four replicate plants of each species were planted in the same manner. Twenty-four tubestock plants per species were used for each treatment at each site, with a total of 432 plants planted.

For each plant, browsing damage was assessed after four weeks by visually estimating the amount of biomass removed by browsers and allocating a corresponding browsing damage score (Table 1). Browsing damage was evidenced by branch loss, and branches or stems stripped of leaves. This rapid assessment method was based on the browsing severity scoring system developed by Bulinski and McArthur (1998) where it was used to assess browsing damage in Tasmanian eucalypt plantations. This system was appropriate for our study due to the scale of the area and number of plants that were assessed.

Additionally, to record browsers present, one trail camera was placed at one of the blocks at each site for the duration of the

experiment. Passive infrared trail cameras (*Little Acorn 5210A*) were used and were set to record three sequential images when motion was sensed with a 1-min delay between each set of images. The cameras were attached to tree trunks at a height of 1–1.5 m above the ground and placed facing a southerly direction to minimise sun glare (Meek et al., 2012). Trees close to wildlife trails and within 4 m of the one of the blocks were selected.

2.4. Survey of revegetated plants two-years after planting

To further assess the effect of cryptic planting, revegetated plants from the Two Million Trees Project were surveyed two-years post-planting. Plants were surveyed in late August–early September 2016 across each of the same three study sites.

Given particularly high rainfall over the survey period, at least 20 plants of each species were selected haphazardly at each site in each of two distinct location types: flooded and non-flooded. Flooded areas were likely to represent extent of flooding in most years, with non-flooded plants unlikely to have experienced flooding since planting. For each plant, it was recorded whether the plant was cryptically planted, which was assessed as whether the plant was growing within the foliage perimeter of a patch of sedges (> 1 m × > 1 m), and whether surface water was present. Each plant was assessed for browsing damage using the same method described for the trial (Table 1), with the addition of browsing damage also evidenced by the absence of new shoots, presence of multiple leaders. An example of browsing damage to *M. squarrosa* is shown with assigned browsing scores in Fig. 2.

2.5. Data analysis

To assess the effect of cryptic planting on browsing damage to plants, we fitted linear mixed models employing restricted maximum likelihood estimation (REML) (Patterson and Thompson, 1971) using GenStat (16th edition, VSN International Ltd, Hemel Hempstead, UK). For the cryptic planting trial, Treatment and Species and their interaction were modelled as fixed effects, and Site, Block nested within Site, and Patch nested within Block were modelled as random effects. For the vegetation survey, Flooding, Treatment and Species and all possible interactions were modelled as fixed effects, and Site modelled as a random effect. Prior to analyses, browsing damage scores were converted to mid-point percentage values (e.g. Browsing Score 1 = 1–25%; mid-point value = 12.5%). Fisher's Least Significant Difference test was used to compare pairwise differences between means where appropriate (i.e. given significant treatment effects). For each analysis, residuals were examined and the assumptions of normality and homogeneity of variance were met.

3. Results

3.1. Cryptic planting trial

Four hundred and thirty-two plants were planted as part of the trial. After four weeks, 406 plants were relocated and assessed for browsing damage. The remaining 26 plants were not found and may have been pulled out by browsers or were simply failed to be relocated.

Cryptic planting significantly decreased the browsing damage experienced by all three species, with cryptically planted plants 22% less browsed overall (cryptic = 15% browsing damage; non-cryptic = 37%) (Fig. 3; Table 2). This effect was particularly apparent for *E. camphora* with cryptically planted *E. camphora* plants 37% less browsed (Fig. 3), whereas cryptically planted *L. lanigerum* plants were 20% less browsed and *M. squarrosa* plants 11% less browsed (Fig. 3).

Overall, *E. camphora* plants were the most browsed of the three species regardless of planting technique, experiencing a mean browsing damage of 43%, whereas *L. lanigerum* and *M. squarrosa* plants had a mean browsing damage of 19% and 16%, respectively (Table 2). Across

Table 1
Browsing damage scoring system adapted from Bulinski and McArthur (1998) with the corresponding percentage ranges of biomass removed by browsers.

Browsing damage score	% Biomass removed
0	0
1	1–25
2	26–50
3	51–75
4	76–100

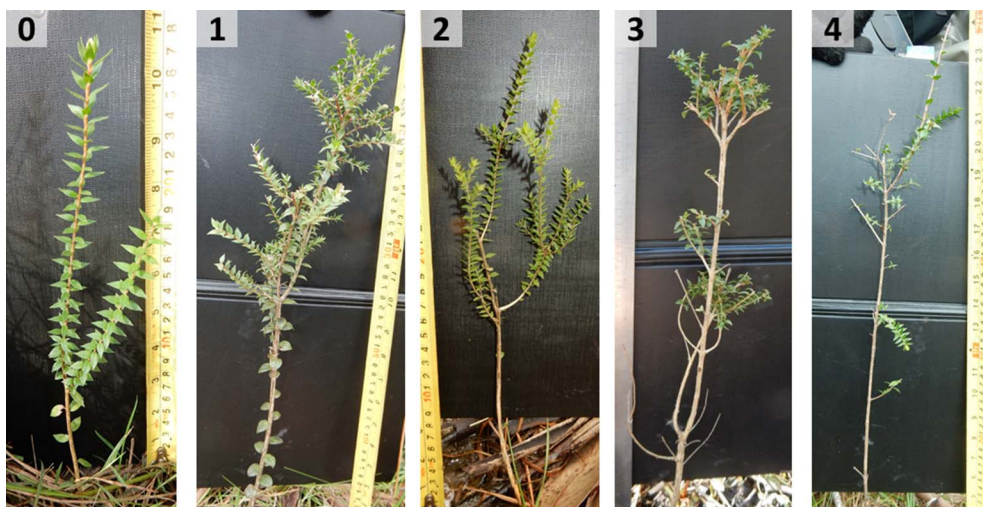


Fig. 2. Photographs of browsing damage to *Melaleuca squarrosa* at Yellingbo Nature Conservation Reserve with assigned browsing damage scores of estimated percentage of biomass removed; left to right, 0 = 0% (no browsing damage); 1 = 1–25% (multiple leaders present); 2 = 26–50% (multiple leaders present and some parts of branches/stems devoid of leaves); 3 = 51–75% (multiple leaders present, many branches/stems devoid of leaves, and few new shoots present); and 4 = 76–100% (multiple leaders present, many branches/stems devoid of leaves and no new shoots present).

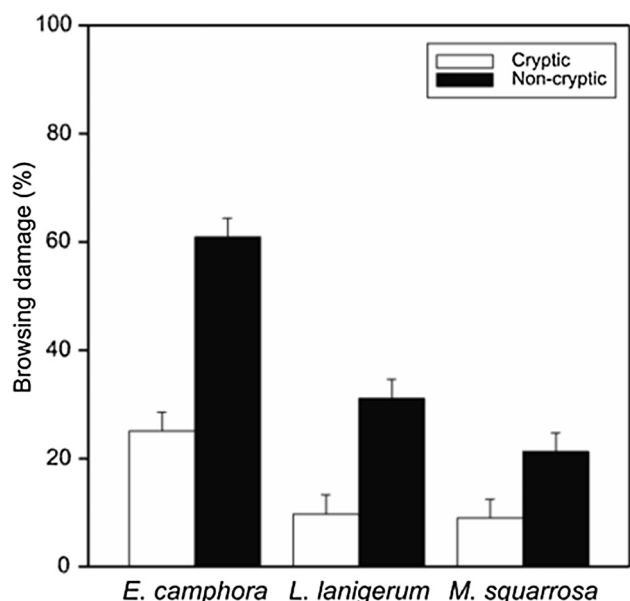


Fig. 3. Mean (+ SE) browsing damage (%) to cryptic and non-cryptic plantings of each of the three species planted.

Table 2

Results of analysis using general linear mixed model with browsing damage as the response variable for the cryptic planting trial. Significant results ($p < 0.05$) are in bold.

Source	ndf	F	P
Species	2	56.15	< 0.001
Cryptic	1	28.24	< 0.001
Species × Cryptic	2	9.00	< 0.001

all three species, woody seedling planted within *C. appressa* patches were particularly less browsed (4%) compared to seedlings planted within patches of other sedge species (20–27%) (N.B. No formal analyses of sedge species was conducted because sedge species varied widely within and between sites).

Images captured by trail cameras showed browsing of planted tubestock by swamp wallabies and the presence of fallow deer, while no sambar deer were captured on camera. In total, the trail cameras captured a total of 12 photo events of these browsers over the four weeks.

3.2. Survey of revegetated plants two-years after planting

Three hundred and fifty-two plants were surveyed across the three study sites two-years post-planting, consisting of 208 non-cryptically planted plants and 90 cryptically planted plants. Twenty plants of each species in both flooded and unflooded areas were surveyed at each site, except at Woori Yallock Creek where only 12 flooded *E. camphora* plants could be located. Cryptically planted plants were on average 17 cm taller than non-cryptically planted counterparts (cryptic = 64 cm tall; non-cryptic = 47 cm tall). Cryptically planted *E. camphora* were the tallest on average at 69 cm tall (compared to 45 cm for non-cryptically planted plants). Cryptically planted *L. lanigerum* were 61 cm tall (compared to 46 cm), and cryptically planted *M. squarrosa* were 64 cm (compared to 52 cm).

Browsing damage was strongly dependent on whether a plant was cryptically planted or not, with cryptically planted plants 23% less browsed than non-cryptically planted plants (non-cryptic = 51% browsing damage; cryptic = 28%) (Fig. 4; Table 3). Whether a plant was flooded or not was not associated with its level of browsing damage. Similar to the cryptic planting trial, *E. camphora* plants were the most heavily browsed of the three species regardless of planting technique, experiencing a mean browsing damage of 71%, whereas *M.*

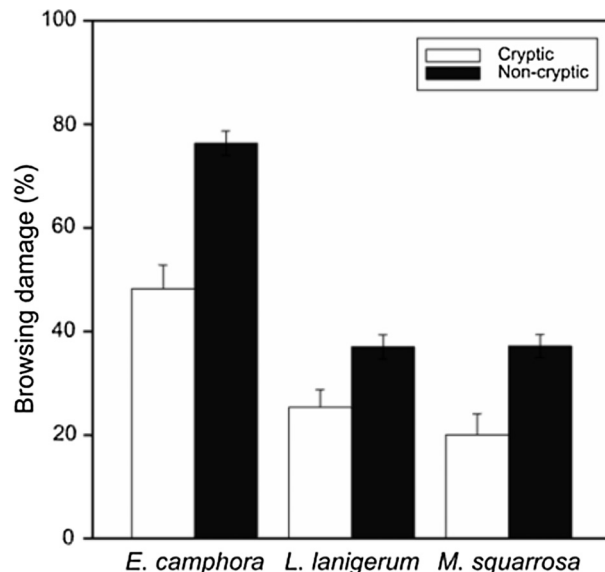


Fig. 4. Mean (+ SE) browsing damage (%) to cryptic and non-cryptic plantings for each of the three species surveyed.

Table 3

Results of analysis using general linear mixed model with browsing damage as the response variable for the vegetation survey. Significant results ($p < 0.05$) are in bold.

Source	ndf	F	P
Species	2	129.45	< 0.001
Flooded	1	0.01	0.908
Cryptic	1	42.74	< 0.001
Species × Flooded	2	1.00	0.370
Species × Cryptic	2	2.57	0.078
Flooded × Cryptic	1	1.48	0.225
Species × Flooded × Cryptic	2	2.11	0.123

squarrosa plants and *L lanigerum* plants had a similar browsing damage of 33% (Fig. 4; Table 3).

4. Discussion

4.1. Cryptic planting reduces browsing

Overall, cryptically planted seedlings (plants planted within the foliage perimeter of large sedges) were significantly less browsed than non-cryptically planted seedlings. We observed this for plants surveyed both four weeks and two years after planting. We suggest that cryptic planting reduces mammalian browsing pressure on woody plant seedlings via unpalatable or less palatable neighbouring plants (such as the sedges) providing protection to palatable seedlings from browsers. In ecological restoration or forestry, cryptic planting may be used when browsers are present as an alternative to costly tree guards or fencing, to provide seedlings with protection from browsers in the first few years of growth.

The reduction in browsing to cryptically planted woody seedlings was likely due to the low palatability of neighbouring plants, as found in previous such studies of plant-animal interactions (e.g. Bakker et al., 2004; Bergvall et al., 2008), and provides evidence for plant associational refuge (Miller et al., 2006; Stutz et al., 2015). In our study, the sharp-edged leaves of the sedges are likely to have acted as a structural defence against browsers, contributing to the low attractiveness of the plantings to browsers. Additionally, the unpalatable sedges may have acted as a visual or olfactory barrier, hiding the plants from browsers. Indeed, higher understorey cover has been associated with delayed detection rates of seedlings by swamp wallabies (Stutz et al., 2015), with dense understoreys thought to interfere with olfactory cues required by swamp wallabies to locate food sources (Bedoya-Pérez et al., 2014).

The degree of browsing damage to woody seedlings was observed to vary depending on the species of the neighbouring plants. For example, when the cover of sedge leaves over a seedling was not continuous or particularly dense, more often the case with *G. sieberiana* and *L. laterale* than *C. appressa*, this may have enabled browsers to browse the woody seedlings without coming into direct contact with the sharp-edged leaves. The variation in protection provided by the different sedge species is also consistent with their relative palatability with studies having found *Carex* spp. to be generally avoided by deer (Forsyth et al., 2010), whereas *Lepidosperma* spp. and *G. sieberiana* have been found in the gut of sambar deer (Forsyth and Davis, 2011). Such differences between nurse plants may contribute to how mammalian browsers spatially select and move between patches, as decisions are dependent on the abundance and type of palatable and unpalatable plants available within a patch (Bergvall et al., 2006). By understanding the browsing preferences of browsers at a specific site, this can help to understand how browsers select between and within patches. This can aid land managers in determining where a woody seedling may have a higher chance of avoiding detection from browsers in order for a plant to establish and persist.

4.2. Could cryptic planting be an effective management tool?

Cryptic planting has the potential to be used as an effective management tool in a range of revegetation activities. By utilising the traits of existing understorey vegetation as protection from browsers, this technique removes economic costs associated with acquiring, installing and maintaining plant protections, which can accumulate in the form of fence repairs and the eventual removal of tree guards. However, the trade-off of less economic cost is that cryptically planted plants may still experience some browsing. Land managers will need to weigh up the costs and benefits of the use of this technique, but as our results show, cryptic planting can provide significant protection from browsing. To increase overall survivability of seedlings when solely using cryptic planting, it may be useful to plant woody seedlings in higher numbers to balance detection rates by herbivores (Stutz et al., 2015).

Even though our results clearly show that cryptic planting may protect seedlings from browsing in the first few years of growth, it is unclear if the effectiveness of the protection decreases once the plants grow taller than the unpalatable plant. Indeed, having taller unpalatable neighbouring plants has been shown to be more effective in reducing browsing on a focal plant when compared to shorter neighbours (Miller et al., 2006). However, minimising browsing within the first 1–2 years after planting is critical to the persistence of a plant (Gill, 1992). Therefore, cryptic planting may provide sufficient protection in the early stages of growth so that plants can persist and eventually become established in the midstorey.

While cryptic planting is dependent on the presence of an existing understorey, it is not limited to ‘infill’ planting (planting within existing vegetation). For example, the use of less palatable nurse plants in revegetation at cleared sites may provide a similar function in protecting seedlings from browsing, such as the use of thistles in forest plantations (Miller et al., 2006). Ideally, unpalatable neighbouring plants would be fast-growing and taller than the woody seedlings in the first few years of growth.

Our research also provides insights into the relative palatability of the woody species studied, with *E. camphora* plants most susceptible to browsing. It is likely that, similar to other *Eucalyptus* spp., this species is highly palatable to mammalian browsers, such as the swamp wallaby and deer (Hollis et al., 1986; Forsyth and Davis, 2011). *L. lanigerum* and *M. squarrosa* plants experienced similar levels of browsing, indicating these species may be similarly less palatable. Nonetheless, browsing pressure can vary between plant species seasonally, as the diets of browsers can change depending on the available resources and nutritional quality of the plants (Moser et al., 2006). However, the differences in browsing damage observed are likely to represent substantial differences in palatability as they were demonstrated over both the short- (1-month) and mid- (2-year) term.

While cryptic planting reduced browsing damage to *E. camphora* by 23%, cryptically planted *E. camphora* still experienced considerable biomass loss. We suggest that when limited resources for plant protection are available, highly palatable species, such as eucalypts, should be prioritised for protection by tree guards or fences. However, when no funding is available for tree guards or enclosures, highly palatable species could be prioritised to be cryptically planted over less palatable species to protect them from browsing. Thus, it is important to identify the browser species present and understand the palatability of the species to be planted to best prioritise appropriate forms of plant protection.

Cryptic planting may provide land managers with a low-cost, yet effective alternative to tree guards and fencing to reduce mammalian browsing damage to planted woody seedlings. This method could improve revegetation outcomes by reducing browsing pressure, leading to increased survival and growth rates of woody seedlings within the important first few years of growth (Gill, 1992). To determine the suitability of cryptic planting at a site, an understanding of the palatability of the existing plants and those to be planted, as well as

knowledge of the type of browsers present is recommended.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2018.02.015>.

References

- Alexander, H.D., Moczygemba, J., Dick, K., 2016. Growth and survival of thornscrub forest seedlings in response to restoration strategies aimed at alleviating abiotic and biotic stressors. *J. Arid Environ.* 124, 180–188.
- Baker, S.E., Johnson, P.J., Slater, D., Watkins, R.W., Macdonald, D.W., 2007. Learned food aversion with and without an odour cue for protecting untreated baits from wild mammal foraging. *Appl. Anim. Behav. Sci.* 102, 410–428.
- Bakker, E.S., Olf, H., Vandenberghe, C., De Maeyer, K., Smit, R., Gleichman, J.M., Vera, F.W.M., 2004. Ecological anachronisms in the recruitment of temperate light-demanding tree species in wooded pastures. *J. Appl. Ecol.* 41, 571–582.
- Bedoya-Pérez, M.A., Isler, I., Banks, P.B., McArthur, C., 2014. Roles of the volatile terpene, 1,8-cineole, in plant-herbivore interactions: a foraging odor cue as well as a toxin? *Oecologia* 174, 827–837.
- Bergvall, U.A., Rautio, P., Kesti, K., Tuomi, J., Leimar, O., 2006. Associational effects of plant defences in relation to within- and between-patch food choice by a mammalian herbivore: neighbour contrast susceptibility and defence. *Oecologia* 147, 253–260.
- Bergvall, U.A., Rautio, P., Sirén, H., Tuomi, J., Leimar, O., 2008. The effect of spatial scale on plant associational defences against mammalian herbivores. *Ecoscience* 15, 343–348.
- Blackney, J.R., Menkhurst, P.W., 1993. Distribution of subspecies of the Yellow-tufted Honeyeater in the Yarra Valley Region, Victoria. *Emu* 93, 209–213.
- Bulinski, J., McArthur, C., 1999. An experimental field study of the effects of mammalian herbivore damage on *Eucalyptus nitens* seedlings. *For. Ecol. Manage.* 113, 241–249.
- Bulinski, J., McArthur, C., 1998. Technical Report No. 9: Browsing Damage in Tasmania: Research Answers To Some Management Questions. Cooperative Research Centre for Sustainable Production Forestry, Hobart, Tasmania.
- Callaway, R.M., 1995. Positive interactions among plants. *Bot. Rev.* 61, 306–349.
- Davis, N.E., Coulson, G., Forsyth, D.M., 2008. Diets of native and introduced mammalian herbivores in shrub encroached grassy woodland, south-eastern Australia. *Wildl. Res.* 35, 684–694.
- Di Stefano, J., 2005. Mammalian browsing damage in the Mt. Cole State forest, south-eastern Australia: analysis of browsing patterns, spatial relationships and browse selection. *New For.* 29, 43–61.
- Forsyth, D.M., Davis, N.E., 2011. Diets of non-native deer in Australia estimated by macroscopic versus microhistological rumen analysis. *J. Wildl. Manage.* 75, 1488–1497.
- Forsyth, D.M., Wilmschurst, J.M., Allen, R.B., Coomes, D.A., 2010. Impacts of introduced deer and extinct moa on New Zealand ecosystems. *N. Z. J. Ecol.* 34, 48–65.
- Gadsen, G., Ashby, M., 1995. Revegetation of Habitat for the Helmeted Honeyeater, *Lichenostomus melanops cassidix*, in the Yarra Valley. *Vic. Nat.* 112–121, 1176.
- Gill, R.M.A., 1992. A review of damage by mammals in North temperate forests: 3. Impact on Trees and Forests. *Forestry* 65, 363–388.
- Hanley, M.E., Lamont, B.B., Fairbanks, M.M., Rafferty, C.M., 2007. Plant structural traits and their role in anti-herbivore defence. *Perspect. Plant Ecol. Evol. Syst.* 8, 157–178.
- Harley, D.K.P., Worley, M.A.W., Harley, T.K., 2005. The distribution and abundance of Leadbeater's possum *Gymnobelideus leadbeateri* in lowland swamp forest at Yellingbo Nature Conservation Reserve. *Aust. Mammal.* 27, 7–15.
- Hollis, C.J., Robertshaw, J.D., Harden, R.H., 1986. Ecology of the swamp wallaby (*Wallabia bicolor*) in north-eastern New South Wales. *I. Diet. Aust. Wildl. Res.* 13, 355–365.
- Hornor, G.J., Cunningham, S.C., Thomson, J.R., Baker, P.J., Mac Nally, R., 2016. Recruitment of a keystone tree species must concurrently manage flooding and browsing. *J. Appl. Ecol.* 53, 944–952.
- Kasel, S., 2008. Eucalypt establishment on former pine plantations in north-east Victoria: an evaluation of revegetation techniques. *Ecol. Manage. Restor.* 9, 150–153.
- Mandujano, C., Montana, C., Mendez, L., Golubov, J., Del, M., 1998. The relative contributions of sexual reproduction and clonal propagation in *Opuntia rastrera* from two habitats in the Chihuahuan Desert. *J. Ecol.* 86, 911–921.
- Meek, P., Ballard, G., Fleming, P.J.S., 2012. An Introduction to Camera Trapping for Wildlife Surveys in Australia. PestSmart Toolkit publication. Invasive Animals Cooperative Research Centre, Canberra, Australia.
- Miller, A.M., McArthur, C., Smethurst, P.J., 2006. Characteristics of tree seedlings and neighbouring vegetation have an additive influence on browsing by generalist herbivores. *For. Ecol. Manage.* 228, 197–205.
- Miller, A.M., O'Reilly-Wapstra, J.M., Potts, B.M., McArthur, C., 2011. Repellent and stocking guards reduce mammal browsing in eucalypt plantations. *New For.* 42, 301–316.
- Moser, B., Schütz, M., Hindenlang, K.E., 2006. Importance of alternative food resources for browsing by roe deer on deciduous trees: the role of food availability and species quality. *For. Ecol. Manage.* 226, 248–255.
- Parker, B.D., 2009. Feeding Biology of Sympatric sambar (*Cervus unicolor*) and Fallow Deer (*Dama dama*) in NE Victoria (PhD Thesis). The University of Melbourne, Creswick, Victoria.
- Patterson, H.D., Thompson, R., 1971. Recovery of inter-block information when block sizes are unequal. *Biometrika* 58, 545–554.
- Pearce, J., Minchin, P.R., 2001. Vegetation of the Yellingbo Nature Conservation Reserve and its relationship to the distribution of the helmeted honeyeater, bell miner and white-eared honeyeater. *Wildl. Res.* 28, 41–52.
- Pfister, C.A., Hay, M.E., 1988. Associational plant refuges: convergent patterns in marine and terrestrial communities result from differing mechanisms. *Oecologia* 77, 118–129.
- Raulings, E., Robinson, J., Reddan, J., 2014. Two Million Trees & the Judith Eardley Wildlife Fund: Draft Revegetation Plan Yellingbo Nature Conservation Reserve. Greening Australia, Melbourne.
- Smit, C., Béguin, D., Buttler, A., Müller-Schärer, H., 2005. Safe sites for tree regeneration in wooded pastures: a case of associational resistance? *J. Veg. Sci.* 16, 209–214.
- Smit, C., Ruifrok, J.L., 2011. From protégé to nurse plant: establishment of thorny shrubs in grazed temperate woodlands. *J. Veg. Sci.* 22, 377–386.
- Sotomayor, D.A., Lortie, C.J., 2015. Indirect interactions in terrestrial plant communities: emerging patterns and research gaps. *Ecosphere* 6 art103.
- Stutz, R.S., Banks, P.B., Dexter, N., McArthur, C., 2015. Associational refuge in practice: can existing vegetation facilitate woodland restoration? *Oikos* 124, 571–580.
- Turner, V., 2003. FFG Act Action Statement: Sedge-rich *Eucalyptus camphora* Swamp. Heidelberg.
- Wilkinson, G.R., Neilsen, W.A., 1995. Implications of early browsing damage on the long term productivity of eucalypt forests. *For. Ecol. Manage.* 74, 117–124.