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Field browsing resistance of Shining Gum and Tasmanian Blue gum seedlings raised under different nutrient regimes in the nursery

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Project C3: Resistance of planting stock to vertebrate browsers

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Introduction

Plantation establishment involves the greatest cost in wood production, whether in broad scale forestry operations or at the relatively small farm scale. However, browsers such as brushtail possum (*Trichosurus vulpecula*), red-bellied pademelon (*Thylogale billardierii*) and Bennett's wallaby (*Macropus rufogriseus*) can severely impede growth of recently planted seedling crops in the absence of expensive fencing or controversial shooting and/or poisoning with sodium monofluoroacetate ('1080'). Increasing seedling resistance to browsing may contribute to a reduced need for these control measures.

Plant resistance to browsing is often observed in the field both between, and within, species. Mammalian browsers are often selective in what they choose to consume, due to the relative benefits (energy, protein) and costs (e.g. plant secondary metabolites requiring detoxification and excretion) of the foliage. Within a plant species, variation in resistance to browsing may be due to leaf chemistry characteristics owing to genetic (O'Reilly-Wapstra et al., 2002; Scott et al., 2002) or environmentally induced (Bryant et al., 1983) differences.

Tree seedlings vary in their palatability to browsers (McArthur et al., 2000), but can suffer greatly reduced growth performance as a result of severe browsing (Bulinski & McArthur, 1999). However, induction of within-species browsing resistance, through manipulation of environmental variables such as light, nutrients and water, is relatively easy in the nursery environment. Different nursery treatments have been shown to affect the resistance of *E. globulus* seedlings to swamp wallaby (*Wallabia bicolor*) browsing, although the basis of this variation was unknown (Marks & Moore, 1998). Similarly, controlled environment trials with possums and pademelons demonstrated that varying environmental resource availability in the nursery affected *E. nitens* seedling intake, up to two-fold, by possums and pademelons (McArthur et al., in press). A subsequent study found similar variation in browsing resistance and further quantified fertilizer regimes required to produce seedlings of defined characteristics (McArthur et al. 2002). Leaf nitrogen and toughness explained most of the variation in intake (McArthur et al. 2002). This was in contrast to studies of mature *E. ovata*, *E. viminalis*, *E. polyanthemos* and *E. sideroxylon* foliage, in which a specific and minor component of leaf secondary compounds, the formylphloroglucinol compounds (FPCs), explained variation in resistance (Lawler et al. 1998; Lawler et al. 2000).

Thus the objectives of this study were to produce 'conventional' (high-nutrient) and 'designer' (low-nutrient) *E. nitens* and *E. globulus* seedlings with careful application of liquid fertilizer and to deploy these seedlings in farm-forestry and forestry sites of varying browsing pressure. Given the critical issue of seedling nutrition, sites were chosen of varying soil quality and seedlings were either fertilized or not fertilised after planting. It was aimed to: 1) evaluate the extent and under what conditions browsing resistance of designer produced *E. globulus* and *E. nitens* seedlings to browsing is maintained and; 2) investigate the effect of post planting fertilizing on resistance.

Materials and methods

Seedlings

Seedlings of *E. nitens* (Hastings seedlot; approx. 200 mm in height) and *E. globulus* (Worrolong seedlot; approx. 85 mm in height) were raised in Lannen 81 trays at Forestry Tasmania's Perth nursery. Early March 2002, 4000 seedlings of each species still in their trays were transported by truck to the CSIRO Forestry and Forest Products outdoor growing area in a controlled temperature container. Within species, seedling trays were randomly allocated to 8 blocks. Half of each block was randomly allocated to high or low fertilizer treatment. Each seedling received approximately 1.25 mg Peters Excel® (N:P:K 20:2.2:6.6; solution concentration 1g.L^{-1}) at each fertilizer application. High fertilizer treatments of each species were fertilized twice weekly until planting. Low fertilizer *E. nitens* were fertilized weekly for 4 weeks and then not at all. Low fertilizer *E. globulus* were fertilized twice weekly for 6 weeks (until approx. 200 mm in height) and then not at all. Seedlings were watered as required with an automatic watering system. Between 6 and 20 April 2002, coinciding with humid, still conditions in the nursery, the fertilized *E. globulus* treatment was attacked by a pathogenic stem fungi that destroyed approx. two thirds of the crop. Fungicide was applied twice but appeared to have no affect. Afflicted seedlings were removed and destroyed. No other treatments were affected. This resulted in there only being adequate *E. globulus* seedlings available for the trial at one site (Dunalley). *Eucalyptus globulus* seedlings used for the second site (Cressy) were stock raised from the Worrolong seedlot during the 2001 season. This stock had been transported to the CSIRO outdoor growing area at the same time as the current-season material and was given exactly the same fertiliser treatments.

Trial sites

Farm forestry sites were selected at Cressy (41°40′40″S, 147°10′00″E) and Dunalley (42°50′30″S, 147°40′50″E) on the basis of different site quality between the sites but relative site homogeneity, in terms of slope, aspect and soil type, within sites. The Cressy site had a sandy soil of low bulk density and water holding capacity, mean annual rainfall and temperature of 637 mm and 11.2 °C respectively, and uniform slope of approx. 5º (low quality site). The Dunalley site had a heavy brown-clay soil of high bulk density, high water holding capacity and mean annual rainfall and temperature of approx. 750 mm and 12.7 °C respectively, and uniform slope of approx. 10º (high quality site). Both sites were weed free and had been ripped and mounded with a Savanah® plough. The Dunalley site was bordered by scrubby woodland and a high pademelon and wallaby population was evidenced by the many scats across the site. In contrast, a relatively low possum population was evidenced by few scats across the Cressy site, that was generally surrounded by cleared land.

The forestry site was in the Florentine Valley on 'Tyenna'Block (146º 28′ E, 42º 39′ S). It had a clay duplex soil, and had been mounded and planted in 2001. No 1080 had been used as the site was part of a study to determine baseline effects of browsing on seedling survival and performance. The existing seedlings were all severely browsed and approx. 5% (on the approx. 5 ha block) had grown greater than around 20-30 cm in height. Scats indicated a moderate population of possums.

Experimental design

All three trials consisted of three blocks, each block containing eight 16-tree plots, one of each randomly allocated treatment. Treatments were high (H) or low (L) fertilizer application in the nursery and were either fertilized (F; 120 g diammonium phosphate, placed in a spade slit 10-15 cm down-slope of the seedling stem) or not-fertilised (NF) after planting. Each of these treatments were then either fenced using wire netting clipped together to form a cage and secured with tent pegs, or not fenced. Seedlings were double planted within cages (=32 tree plots) to allow for destructive sampling of fenced (unbrowsed) seedlings.

Monitoring and chemical analyses of seedlings

Seedlings were planted on 1, 9 and 18 July 2002 at Dunalley, Tyenna, and Cressy, respectively. were Unfenced seedlings were monitored for apical tip browsing, % foliage removed and seedling height. This occurred weekly for up to 10 weeks after planting, depending on rate and severity of browsing. At planting, 1, 2, 3, 6, and up to 10 weeks after planting, eight seedlings of each fenced treatment were randomly harvested from each trial, transported on ice (maximum 2 h) before being placed in a –20 ºC freezer. Seedlings were then randomly allocated to three replicates within trial, treatment and sampling date.

Foliage within each replicate was stripped and allocated to five fractions for analysis of (1) nitrogen and phosphorus content, (2) dry matter and fibre (data not shown), (3) chlorophyll and carotenoid content, (4) phenolic and FPC content and (5) essential oil content as described in Close et al (2001) and McArthur et al (In press). Due to limited material, samples of post-plant fertilized (F) and not post-plant fertilised (NF) treatments were pooled within each nursery treatment (H or L) for chemical analysis. The amount of leaf material available for fibre analyses per replicate at Dunalley and Cressy was not adequate to enable accurate quantification. For this reason material from Dunalley was pooled across plots within each sampling date, and that from Cressy was pooled across plots and sampling dates (into weeks 0, 1, 2, and 3, and 6 and 10).

Statistical analysis

Browsing data were analysed for effects of nursery (H and L) and field (F and NF)) fertilizing using PROC GLM for repeated measures (SAS Institute Inc., 1989), with plot as the unit of replication. Data were transformed when necessary before analysis to satisfy assumptions of normality and homoscedasticity (Zar, 1996). Change in height from planting to the end of trial was analaysed using PROC GLM (SAS Institute Inc., 1989). Analysis of variance (PROC GLM) indicated that there were rarely any differences between effects of field fertilizing on leaf chemistry, within sampling dates. Thus leaf chemistry results for field fertilizing treatments were pooled and only 0 and 10 weeks after planting data presented for purposes of clarity.

Results and discussion

Effect of fertiliser treatments on leaf chemistry

Nitrogen

The high nutrient seedlings had around 3-, 1.5- and 2.3-times more N than the low nutrient conspecifics at planting at Cressy, Dunalley and Tyenna, respectively (Table 1a, b, c). The difference in N between seedlings planted at Cressy and Dunalley was likely due to the seedlings planted at Cressy being relatively old, giving them more time to retranslocate, grow and dilute the available N.

Table 1. Nitrogen (N; % DM), chlorophyll ($mg.gDM^{-1}$), dry matter (%), neutral detergent fibre (NDF; % of total DM), acid detergent fibre (ADF; % of total DM), lignin (% of total DM), hydrolysable tannins (HTs; $mg.gDM^{-1}$ tetra-galloylglucose equilavents), formylphloroglucinols (FPCs; $mg.gDM^{-1}$), and total essential oils (TIC $ratio.gDM^{-1}$) 0 and 10 weeks after planting in low and high nutrient treated *E. globulus* seedlings at (a) Cressy and (b) Dunalley and (c) in *E. nitens* seedlings at Tyenna.

(a)	**Low nutrient**		**High nutrient**	
	0	**10**	**0**	**10**
N	0.43 (± 0.15)	1.62 (± 0.15)	1.62 (± 0.15)	1.51 (± 0.15)
Chlorophyll	0.59 (± 0.27)	1.17 (± 0.27)	3.34 (± 0.27)	2.21 (± 0.27)
Dry matter	39.0	50.4	37.1	47.2
NDF	24.4	32.0	21.4	23.9
ADF	23.1	28.0	18.7	22.5
Lignin	10.3	15.2	14.6	14.4
HTs	279 (± 28)	326 (± 28)	143 (± 28)	266 (± 28)
FPCs	28.5 (± 5.6)	22.2 (± 5.6)	40.5 (± 5.6)	13.8 (± 5.6)
Oils	2.82 (± 1.03)	1.09 (± 1.03)	0.98 (± 1.03)	1.63 (± 1.03)

(b)	**Low nutrient**		**High nutrient**	
	0	**10**	**0**	**10**
N	0.90 (± 0.08)	1.34 (± 0.08)	1.26 (± 0.08)	1.54 (± 0.08)
Chlorophyll	1.75 (± 0.29)	2.46 (± 0.29)	3.31 (± 0.29)	2.84 (± 0.29)
Dry matter	32.7	36.7	34.9	42.9
NDF	22.6	21.8	24.7	21.0
ADF	22.9	20.7	22.1	19.8
Lignin	5.2	5.2	5.3	5.0
HTs	379 (± 22)	321 (± 22)	235 (± 22)	300 (± 22)
FPCs	45.6 (± 5.8)	30.2 (± 5.8)	45.2 (± 5.8)	37.1 (± 5.8)
Oils	8.47 (± 1.86)	7.69 (± 1.86)	9.99 (± 1.86)	12.97 (± 1.86)

(c)	Low nutrient		High nutrient	
	0	10	0	10
N	0.61 (± 0.08)	0.63 (± 0.08)	1.41 (± 0.08)	0.85 (± 0.08)
Chlorophyll	1.32 (± 0.29)	1.18 (± 0.29)	3.43 (± 0.29)	1.94 (± 0.29)
Anthocyanin	low	high	low	high
Dry matter	39.8 (± 0.01)	46.3 (± 0.01)	39.8 (± 0.01)	50.4 (± 0.01)
NDF	20.1 (± 3.7)	20.5 (± 3.7)	23.6 (± 3.7)	20.2 (± 3.7)
ADF	18.1 (± 2.5)	18.6 (± 2.5)	21.4 (± 2.5)	18.5 (± 2.5)
Lignin	6.0 (± 0.75)	5.8 (± 0.75)	9.3 (± 0.75)	6.9 (± 0.75)
HTs	545 (± 55)	555 (± 55)	386 (± 55)	515 (± 55)
FPCs	13.1 (± 2.2)	11.5 (± 2.2)	17.3 (± 2.2)	11.7 (± 2.2)
Oils	0.49 (± 0.26)	1.20 (± 0.26)	0.94 (± 0.26)	1.92 (± 0.26)

Chlorophyll and anthocyanin

Foliar total chlorophyll content is generally proportional to foliar N levels. It follows that trends and relative differences between treatments in chlorophyll content observed here were generally very similar to that of N. However, total chlorophyll content in high nutrient *E. nitens* at Tyenna decreased to a relatively greater degree from 3 to 10 weeks after planting, than N levels did during the same period. This is consistent with the high plasticity of *E. nitens* pigment levels with respect to abiotic conditions. *E. nitens* seedlings have been shown to significantly decrease chlorophyll content within 2 days, in order to decrease light absorption under low temperature conditions, and to significantly increase anthocyanin content within 8 days, to screen out light (Close et al. unpublished); low temperatures occurred at Tyenna during this period - snowfall prevented monitoring in early October. The observed decrease of chlorophyll content, and visible increase in anthocyanin content, had a large effect on the appearance of foliage. Leaves, where anthocyanin did not mask the chlorophyll, were noticeably lighter in their shade of green. In addition, many leaves were clearly red, due to the increase in anthocyanin.

Lignification

One factor in the cost of foliage consumption by many herbivores is leaf toughness, which is affected by dry matter content, cellulose, hemi-cellulose and lignin levels. High levels of foliar N are often associated with less lignification per unit leaf area (Evans and Poorter 2001). In contrast to this generalization high nutrient treatments generally had relatively high dry matter content in this experiment. However, this did not translate to greater fibre or lignin contents, except for the seedlings planted at Cressy. This may therefore be a trait inherent to seedlings: young leaf material is relatively 'soft', regardless of nutrient status and it may be this characteristic that makes young leaf material generally attractive to herbivores.

Plant secondary compounds

Other characteristics that confer resistance of leaf foliage to browsing are plant secondary compounds such as hydrolysable tannins (HTs) and formylphloroglucinol compounds (FPCs). HTs can decrease digestibility, through the precipitation of protein, and may be toxic if metabolized (Foley et al., 1999). FPCs constrain intake apparently by providing a toxic load. HTs were 2.0-, 1.6-, and 1.4-times less abundant in high- compared with low-nutrient seedlings for Cressy, Dunalley and Tyenna, respectively, at planting. Levels generally increased during the experimental period in high nutrient seedlings, but remained relatively constant in low nutrient seedlings, so that they had more or less converged by 10 weeks after planting. In contrast, levels of FPCs were relatively similar between all treatments and during the experimental period. Thus, seedlings high in HTs at planting were browsed less, particularly initially, and differences in browsing preference were greatest at Cressy where differences in HT levels were most pronounced. Thus, trends in HTs were consistent with observed browsing patterns. However, the largest differences in browsing preference and HT coincided with the lowest browsing pressure at Cressy. Whilst HTs may reduce intake on an individual browser basis, less overall seedling damage is not apparent on sites of high browsing pressure as the accumulated damage of many individuals partaking in, albeit small, meals is high. Further, it is not known whether the HT levels in seedlings were high enough to affect browsing: levels observed were relatively low c.f. mature foliage (e.g. Lawler et al. 2000). In contrast to HTs, FCP levels did not correspond with browsing preference. FPC levels did not vary with time after planting (results not shown) and so presumably did not contribute to determining the different browsing patterns observed between low and high nutrient seedlings.

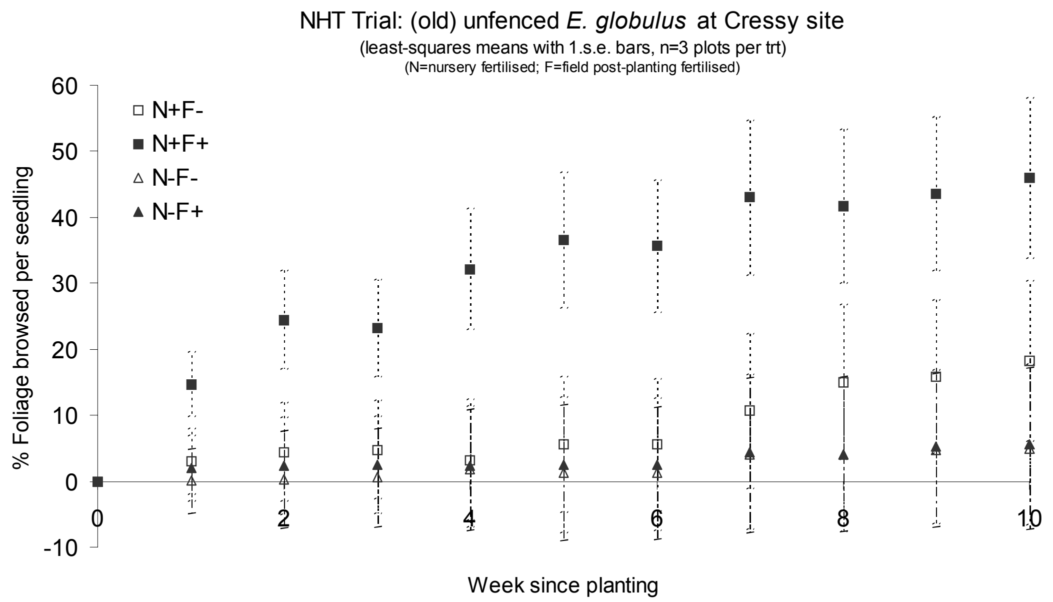
At Tyenna and Dunalley, total essential oils were generally similar between treatments and did not vary with time. In contrast, oils steadily decreased throughout the experiment at Cressy in high fertilizer treatments (results not shown). This result, observed in *E. globulus*, is in contrast to that observed in *E. nitens* by Close et al. (2002) where essential oils were proportional to foliar N content: N levels remained constant during the experimental period at Cressy. Essential oils have been shown to provide a cue to levels of FPCs, but not to HTs, in *E. ovata*, *E. viminalis*, *E. polyanthemos* and *E. sideroxylon* foliage (Lawler et al. 1998; Lawler et al. 2000). However, it would appear that essential oils were probably not a cue to FCP levels in this study, as FCPs remained relatively constant at Cressy in contrast to essential oils.

Effect of fertilizer treatments on browsing over time

We found that seedlings produced under a low fertiliser regime in the nursery were less likely to have their apical buds removed (Cressy $F_{1,8} = 4.59$, $P = 0.0646$; Tyenna $F_{1,6} = 10.57$, $P = 0.0174$) and had less foliage removed (Cressy $F_{1,8} = 6.74$, $P = 0.0318$; Tyenna $F_{1,6} = 10.29$, $P = 0.0184$; Figures 1a, b, c) than high nutrient-regime seedlings. These outcomes were most pronounced under relatively low browsing pressure (Cressy), intermediate under moderate browsing pressure (Tyenna) and were weak under high browsing pressure (Dunalley fertiliser effects not significant). Total % of foliage removed was around 45 and 5 % in H-F and L-F seedlings, respectively, at 10 weeks after planting at Cressy. At Tyenna, large differences were evident at 1 and 2 weeks after planting but levels of damage had converged to close to 100% by 6 weeks after planting. At Dunalley, the trend of less damage to low fertilized seedlings in the nursery was evident one week after planting, but all seedlings had been completely browsed by 2 weeks after planting.

Figure 1. Average % foliage removed from low and high fertilized seedlings in the nursery, either fertilized or not in the field: *E. globulus* seedlings at (a) Cressy, (b) at Dunalley and, (c) *E. nitens* seedlings at Tyenna.

(a)



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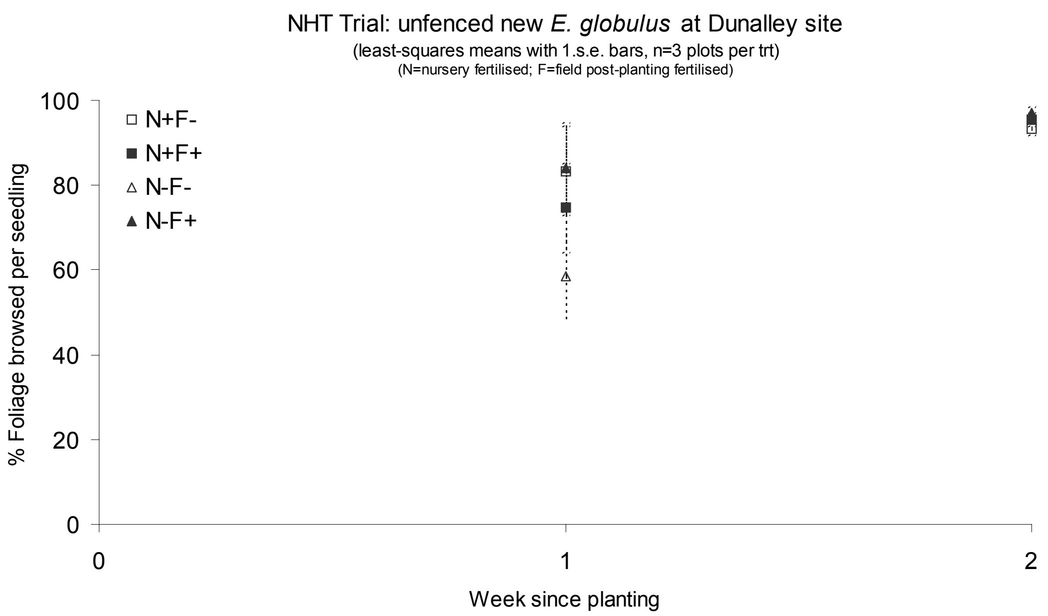

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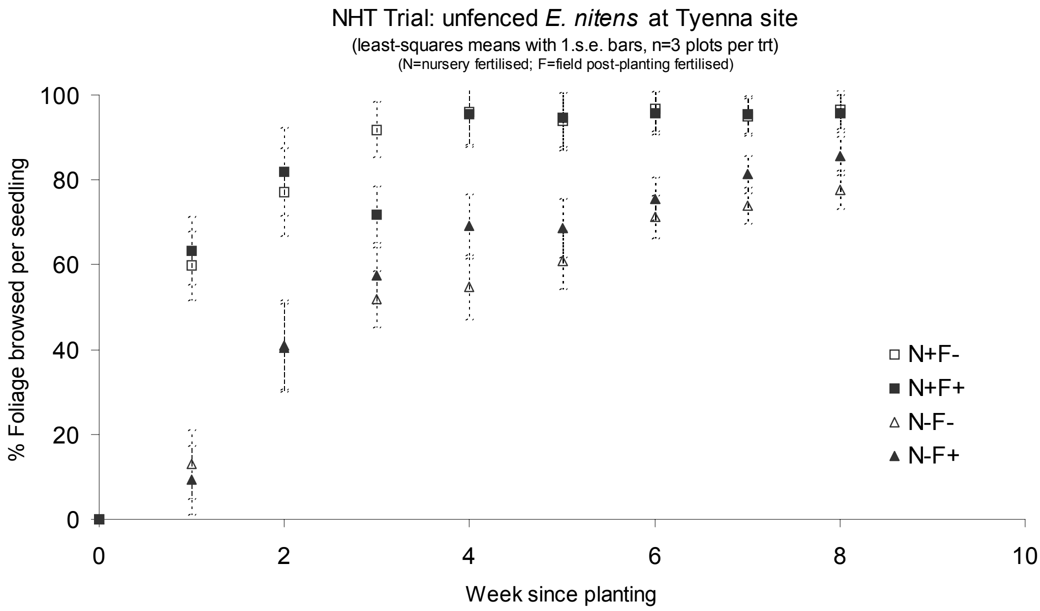

Post-planting fertiliser did not have a significant effect on browsing resistance, although at Cressy (low quality, sandy soil site), fertilising appeared to increase the amount of foliage browsed in H-F c.f. H-NF but not in L-F c.f. L-NF seedlings (Figure 1a). Root growth potential is greater in high, compared to low, nutrient status seedlings (Close 2001). Thus, the relatively vigorously growing roots of high nutrient seedlings may have accessed the applied fertilizer soon after planting, whereas the relatively low-vigour roots of low nutrient seedlings may not have accessed the applied fertilizer during the period of the experiment. However, this did not translate to positive height growth: height was generally negative with time after planting at all sites due to browsing of apical buds and the upper portions of stems (see Appendix 1).

Of the leaf chemistry characteristics investigated, N was strongly affected by nursery treatment. All other factors remaining equal, herbivores should browse material high in nitrogen (N) (i.e. protein) to maximize the benefit:cost ratio of browsing. Further, that browsing continued to increase at Tyenna during 3 to 10 weeks after planting (when chlorophyll decrease and anthocyanin increase markedly altered the appearance of leaves) may indicate that browsers do not use visual green- or red-leaf colour cues to select for material suitable for consumption. However, whilst lignification was similar between treatments, or greater in high nutrient seedlings that were preferentially browsed at Cressy, levels of HTs, but not FCPs, varied between treatments in a pattern consistent with trends in browsing. Thus, the combination of foliar N and HT levels of seedlings arising from the pre-planting nursery treatment, may be the primary factors that explain the general trends in browsing preference observed.

Conclusions

That the principal of less damage to seedlings of relatively low nutrient status applied to both *E. nitens* and *E.globulus* indicates that it is a technique that may work for other species raised in nurseries for farm forestry/revegetation purposes. However, the trend for greater damage to high nutrient seedlings that were fertilized after planting at Cressy, may indicate that post-planting fertiliser should not be applied to tree seedlings until they are tall enough to avoid apical bud browsing and/or have become sufficiently robust to browsing through leaf morphological and chemical traits. Overall, damage sustained was acceptable to low, but not high, nutrient seedlings at 10 weeks after planting under low browsing pressure at Cressy. This outcome may compare favourably to that of using 1080 poison where browsing animal populations can return to pre-planting levels by 6 weeks after planting (Le Mar and McArthur 2001). However, whilst low nutrient seedlings were less browsed soon after planting, the effects were short lived where browsing pressure was high. Given this, the technique is probably going to be most beneficial when used on low to medium browsing pressure sites in combination with other 'ecologically friendly' methods of browsing animal control, such as provision of an alternative (cover) crop and/or decreased apparancy using native vegetation 'screens'. It must be cautioned though, that seedlings produced under low nutrient conditions in the nursery may have reduced growth potential after planting onto low nutrient sites, or when planted pre-winter, due to N deficiency. Thus, there is a trade-off that managers need to consider: the added resistance of low nutrient seedlings to browsing vs. lost growth potential and vice versa for high nutrient seedlings.

Acknowledgements

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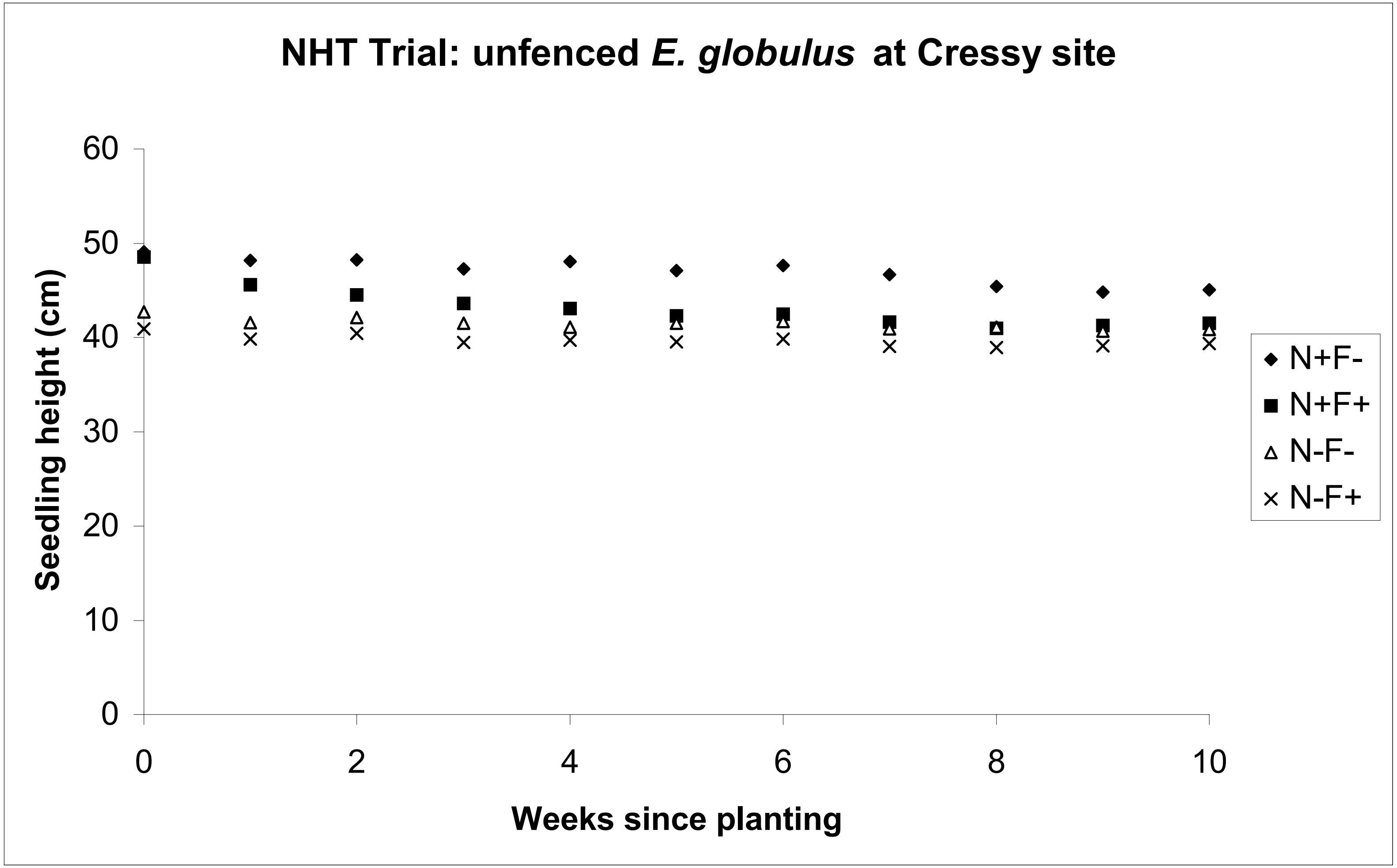
Appendix 1. Seedling height since planting of low and high fertilized seedlings in the nursery, either fertilized or not in the field: (a) *E. globulus* seedlings at Cressy and (b) at Dunalley and, (c) *E. nitens* seedlings at Tyenna.

(a)



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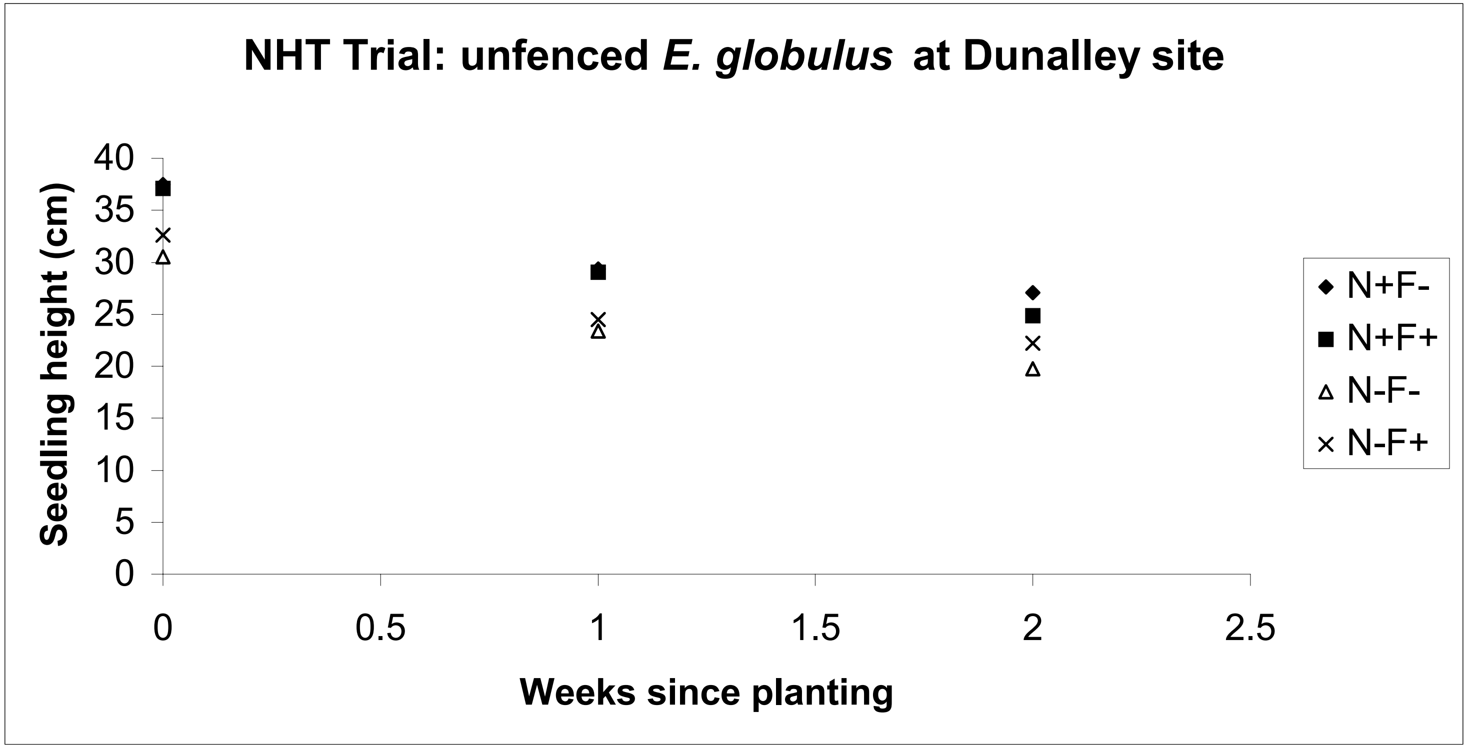
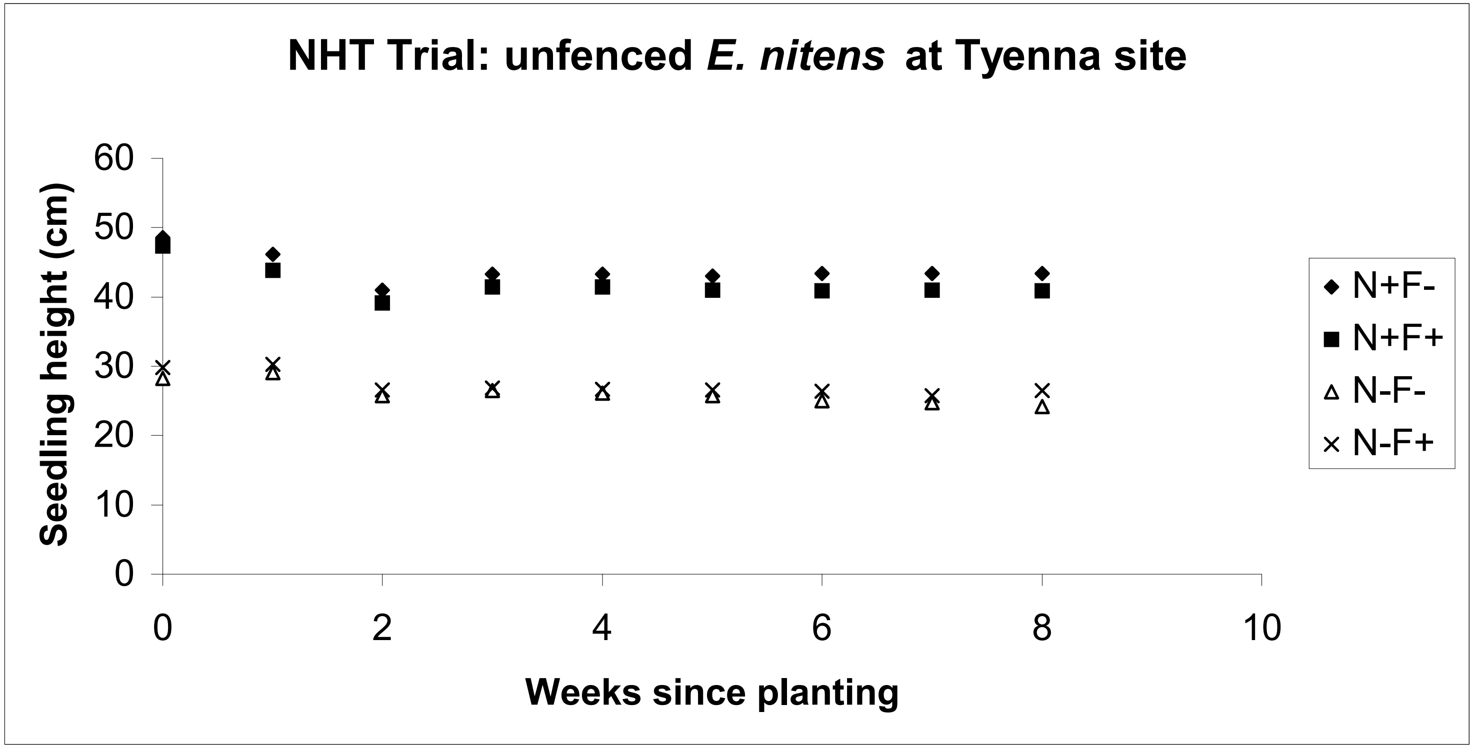

NHT Trial: unfenced *E. globulus* at Dunalley site
Seedling height (cm)
0
5
10
15
20
25
30
35
40
0
0.5
1
1.5
2
2.5
Weeks since planting
N+F-
N+F+
N-F-
N-F+

(c)


NHT Trial: unfenced *E. nitens* at Tyenna site
Seedling height (cm)
60
50
40
30
20
10
0
0
2
4
6
8
10
Weeks since planting
N+F-
N+F+
N-F-
N-F+