The effect of tree spacing on the production of flowers in *Eucalyptus nitens*

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Summary

The effect of spacing on the production of flowers and capsules in *Eucalyptus nitens* was studied in two spacing trials located in northern Tasmania. Tree density in these trials ranged from 468 to 4216 stems ha^{-1}. Reproductive structures were collected in litter traps and these data were used to calculate reproductive output on a per tree and per hectare basis. Between 8735 (5-y-old site, 1333 stems ha^{-1}) to 234 098 (13-y-old site, 1082 stems ha^{-1}) flowers were produced per hectare over a single flowering season at these two study sites at the planting densities expected of a pulpwood plantation. This represented 8 and 211 flowers per tree respectively. As tree density decreased, the production of flowers and capsules increased on both a per-tree and per-hectare basis. It is estimated that the number of flowers per hectare is likely to be anywhere between between 1.4 and 10-fold greater under the spacing expected in sawlog regimes (250 trees ha^{-1}). This difference in reproductive output between plantations of *E. nitens* that use different spacing regimes is one of the many factors that need to be considered in assessing the risk of wilding establishment or hybridisation with adjacent native eucalypts.

Keywords: flowering; stand density; spacing; reproductive traits; genetic contamination; *Eucalyptus nitens*

Introduction

The eucalypt plantation estate in Australia is rapidly expanding to meet the Australian Government's 2020 targets (Anon. 1997; Wood *et al*. 2001). The major expansion to date has been in temperate Australia involving *Eucalyptus globulus* and *E. nitens* plantations (Wood *et al.* 2001), but the expansion is extending into subtropical (Nikles and Lee 1998) and low-rainfall (Harwood and Arnold 1999) zones. Environmental remediation is a major impetus for the expansion into low-rainfall and salt-affected areas (Marcar *et al.* 1995; O'Neill 1999). However, it is important to understand the overall environmental impacts of such plantings through their on- and off-site effects on factors such as water availability (Vertessy 1999; Vertessy and Bessard 1999) and biodiversity (Strauss 2001). A particular concern is the impact of seed (wildling establishment) or pollen (hybridisation) dispersal, and consequently gene flow, from eucalypt plantations into adjacent native eucalypt forest of conservation value (Standards Australia 2003; Barbour *et al.* 2003; Potts *et al.* 2003, Southerton *et al.* 2004). Understanding factors affecting flower production in plantations will be important if management strategies are required to minimise such off-site effects.

Reducing stand density is known to increase flower production in forest trees (Arista and Talavera 1996; Smit and Rethman 1998). In plantation silviculture, the spacing between trees can be varied to suit the intended purpose and the environment of the plantation. Wide spacing between trees may be used in agroforestry systems (Bird *et al.* 1994) or in seed orchards (Moncur 1998). In contrast, growing trees closely together can maximise total wood volume per hectare (Coetzee and Naicker 1998). In low-rainfall environments, trees should be grown at spacings, usually wide, that maintain a sustainable water use regime (White *et al.* 2001). Spacing may also be altered through the life of a plantation. Close spacing during early growth is used to minimise branching and encourage apical dominance in trees destined for sawlogs (Neilsen and Gerrand 1999), then spacing is increased through thinning to promote diameter growth of the remaining trees (Medhurst and Beadle 2000) to produce larger logs.

Eucalyptus nitens is the major hardwood plantation species in Tasmania where it is being grown under both pulpwood (Tibbits *et al*. 1997) and sawlog (Neilsen and Gerrand 1999) silviculture regimes. For the production of *E. nitens* pulpwood, it is recommended that plantations are established at 1333 stems ha^{-1}, not thinned and have a rotation length of typically 15 y (Neilsen 1990). In contrast, *E. nitens* plantations grown for sawlogs are established at a slightly lower stocking rate of 1100 stems ha^{-1} (Neilsen and Gerrand 1999), and then thinned at around 5–7 y of age to 200–300 stems ha^{-1} (Medhurst *et al.* 2001; Pinkard and Neilsen 2003). The present paper uses two silviculture spacing trials, established to determine optimal spacing for tree growth, to study the effect of variation in tree spacing on flower production by *E. nitens* at an individual-tree and per-hectare level.

Methods

Study sites

Two *E. nitens* spacing trials were used in this study. The first was established in 1992 by Forestry Tasmania at a site near Castra, 15 km south of Ulverstone in northern Tasmania (146°08'E, 41°18'S) using seed derived from the Toorongo provenance of central Victoria. The trial was established on a fertile, ex-pasture site, which received a mean annual rainfall of 1250 mm and was 310 m asl. Planting took place in late winter 1992 when 24 experimental plots were established, each 30 m × 30 m at one of six different planting densities replicated four times in randomised complete blocks. In the centre of each experimental plot was a 25-tree measurement plot (Neilsen and Gerrand 1999).

The second site was established in 1984 by Australian Pulp and Paper Mills Limited (now Gunns Limited) at a site known as Ringwood, 34 km south of Burnie in north-western Tasmania (145°39'E, 41°19'S). The seed was derived from a pool of 21 open-pollinated seedlots collected from the Upper Yarra region in Victoria that is also part of the Toorongo provenance. This trial was established in an area previously covered with eucalypt-myrtle forest, which received a mean annual rainfall of 1800 mm and was 550 m asl (Wang *et al*. 1998). The site was planted in early summer 1984 in a Nelder design (Nelder 1962) that consisted of 35 radiating spokes separated by 3° at their origin. Each spoke was intersected by 24 concentric circles of increasing radius. Each circle was spaced such that the increase in radius was the same as the distance separating two spokes at the point where the circle intersected the spokes. This design produced a constant rectangularity as the spacing increased with increasing distance from the origin of the spokes, and inter-circle spacings ranged from 1.5 m to 5.0 m (T.A. Fisk and T.W. Docking, Forestry and Timber Division, APPM Ltd, Burnie, unpublished data, 1984).

Both sites were intensively managed before and after planting to suppress weed competition and browsing. Any deaths up to six months of age were replaced with surplus stock of the same origin at both trials (T.A. Fisk and T.W. Docking loc. cit.; Neilsen and Gerrand 1999).

Assessment of flowers and capsules

In mid-November 1997, litter traps to collect floral parts (i.e. opercula, aborted flowers and immature fruit, and shed mature capsules) that fell from the canopy were established in both the Castra and Ringwood spacing trials, about 5 and 13 y after planting respectively. This time corresponded to the beginning of the *E. nitens* flowering season at these sites. In the Castra trial, one trap was randomly placed in the measurement plot of five of the six spacings in each of the four replicates (Table 1) for a total of 20 traps. In the Ringwood trial, five traps were placed randomly between spokes in each of 5 arcs corresponding to planting densities shown in Table 1 for a total of 25 traps.

The litter traps were constructed from Weathashade® 70% shade cloth suspended at each corner from 80-cm galvanised steel posts. Each trap was of a size and shape such that each of the four corners rested against the trunk of a tree; thus the area sampled was equivalent to the spacing of each tree. The canopy sampled was equal to one quarter of that of each of the four trees surrounding the trap, and therefore considered equivalent to one whole tree. The centre of each trap was secured, using a steel wire, to a pin embedded in the ground; this formed the trap into a shallow cone and prevented the contents of the trap being blown out.

The litter in each trap was collected at intervals of about seven weeks from mid-November 1997 until the final collection in mid-November 1998, just prior to the onset of the next season's flowering. The litter was air dried prior to hand sorting. In each collection, the numbers of (i) opercula, (ii) aborted opened flower buds and immature capsules (valves still closed) and (iii) mature capsules (valves opened) were counted. Each operculum collected was directly equivalent to an open flower in the canopy. The annual totals for each trap for the reproductive structures were calculated prior to analysis. The open flowers and immature capsules were from the same flowering season as the opercula, whereas the mature capsules were mainly from previous flowering years.

Trial growth measurements

In May 1997 (4.5 y after planting) the diameter at breast height over bark (dbhob) of all trees in the measurement plots of the Castra trial were recorded and plot means calculated. In December 1998 (14 y after planting) all trees in the Ringwood trial were measured for dbhob.

Statistical analysis

The annual totals for each reproductive structure (i–iii above) for each trap represented the total for a single tree, and total values per hectare were calculated from the area covered by each trap. A statistical model was then fitted for each reproductive structure (i–iii) and for estimates of the percentage of flowers which opened but were lost before reaching seed maturity (100 × ii / i). Analysis was also undertaken to examine and remove the effect of tree size by including mean dbhob as a covariate. For the Castra trial, plot means for dbhob were used, whilst for the Ringwood trial mean dbhob for the trees at each corner of the trap were used. These measurements were also used to analyse the spacing effect on dbhob alone. The model fitted to the data for the Castra trial was

$$\text{trait} = \text{mean} + \text{rep} + \text{spacing} + \text{error}, \tag{1}$$

whilst the model fitted to the data from the Ringwood trial was

$$\text{trait} = \text{mean} + \text{spacing} + \text{error}. \tag{2}$$

In each analysis the data was $\log_{10}$-transformed to optimise the

Table 1. Planting densities and respective tree spacing of the Castra (Forestry Tasmania) and Ringwood (Gunns Limited) trials examined for flower and capsule production

Trial	Planting density (stems ha^{-1})	Spacing between trees (m)
Castra	500	5.00 × 4.00
	833	4.00 × 3.00
	1010	3.30 × 3.00
	1333	3.00 × 2.50
	1667	3.00 × 2.00
Ringwood	468	4.62 × 4.62
	730	3.70 × 3.70
	1082	3.04 × 3.04
	2500	2.00 × 2.00
	4216	1.54 × 1.54

normality of the residuals and homogeneity of the error variances, then back-transformed for graphical presentation on a per-tree and per-hectare basis (Fig. 1). The respective models (Eqns 1 and 2) were fitted using the PROC MIXED procedure in SAS Version 9.2 (SAS Institute 1992) to generate the specific contrasts, least squares means and standard errors. For each trait, specific *a posteriori* contrasts between the least-square means of each spacing class were undertaken using the Tukey–Kramer adjustment for multiple comparisons. The relationship between tree spacing and operculum numbers per tree and per hectare was also modelled using linear regression analyses undertaken with the PROC REG procedure of SAS Version 9.2. Pearson correlations between the number of mature capsules and the number of opercula per hectare were carried out using the PROC CORR procedure in SAS Version 9.2. The data from the fifth trap in the 730 stems ha^{-1} section of the Ringwood trial were excluded from the analysis as this trap was located in an area of the trial found to be prone to water-logging and very few reproductive structures were trapped over the whole year. Actual regression equations used are not shown here, though variables are italicised in the text.

Results

Increased tree density significantly reduced the number of flowers per tree at both the 5-y-old Castra site ($F_{4,12} = 4.15$; $P = 0.025$) and to a greater extent in the 13-y-old Ringwood site ($F_{4,19} = 21.7$; $P < 0.001$) where a broader range of tree density classes was represented (Fig. 1). This trend was also evident on a per-hectare basis at both sites (Castra $F_{4,12} = 2.2$; $P = 0.126$ and Ringwood $F_{4,19} = 6.1$; $P = 0.003$) (Fig. 1). At both sites a linear regression using the number of stems per hectare (*stems.ha*$^{-1}$) accounted for a statistically-significant component of the variation in the $\log_{10}$-transformed number of opercula per hectare (*op*) (Castra, $\log_{10}(op + 1) = 5.56 - 0.0009197\ stems.ha^{-1}$, $r^2 = 0.23$, $F_{1,18} = 5.4$, $P < 0.05$; Ringwood, $\log_{10}(op + 1) = 5.817 - 0.000226\ stems.ha^{-1}$, $r^2 = 0.43$, $F_{1,22} = 16.3$; $P < 0.001$).

At 5 y of age at Castra, the density of 1333 stems ha^{-1} used for pulpwood plantations resulted in relatively low levels of flowering, which averaged 8 flowers per tree or 8735 flowers ha^{-1} (back-transformed $\log_{10}$ means presented in Fig. 1). This level increased to an average of 270 flowers per tree and 134 895 flowers ha^{-1} at the lowest tree density of 500 stems ha^{-1}. At the 13-y-old Ringwood site, observations from the 1082 stems ha^{-1} planting density could be considered representative of a later-age pulp plantation when accounting for mortality. Here, the flowering level was 211 flowers per tree or 234 098 flowers ha^{-1} (Fig. 1). At the lowest tree density of 468 stems ha^{-1}, this level increased to an average of 1334 flowers per tree and 658 414 flowers ha^{-1}. Extrapolation of the data for the Ringwood site to a density of 250 stems ha^{-1} (i) assuming that the number of flowers per tree remained unchanged or (ii) using the linear regression equation above, gives an estimated production of 333 438 or

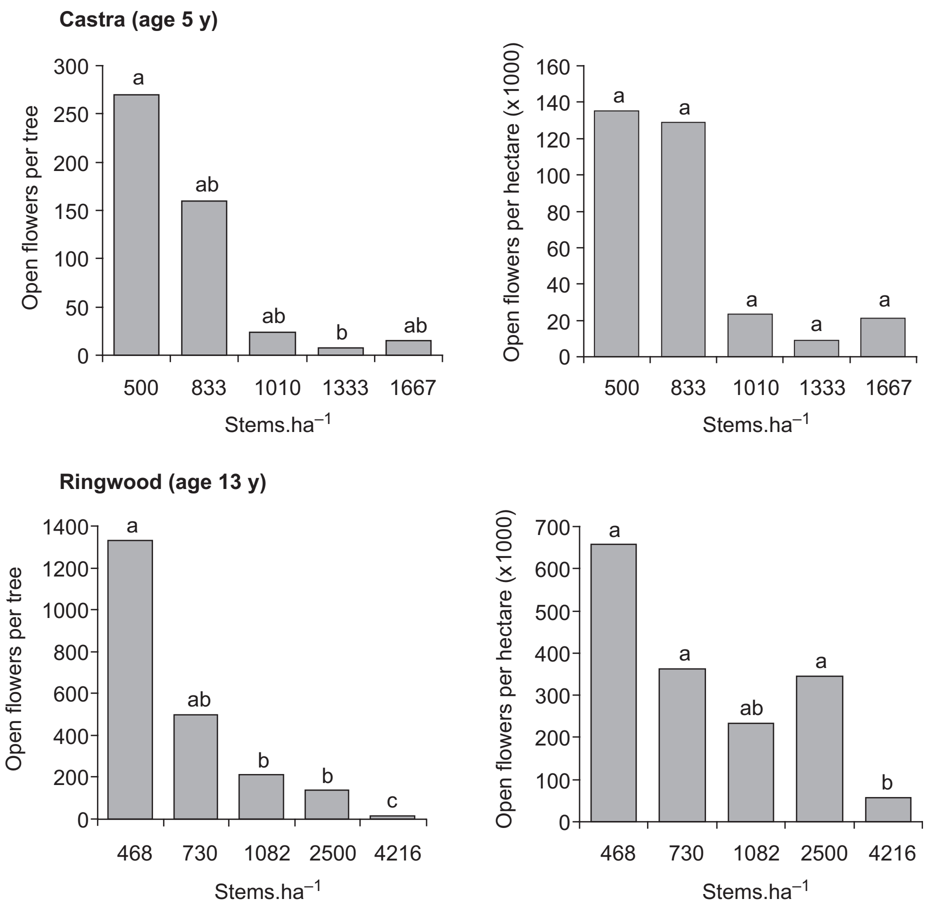

Figure 1. Mean number of *E. nitens* flowers that opened (based on opercula collected in litter traps) at different planting densities in the Castra and Ringwood trials. Results are represented on a per-tree and per-hectare basis for both trials and have been back-transformed from $\log_{10}$-transformed values. Means with the same letter are not significantly different ($P > 0.05$) based on Tukey–Kramer adjustment for multiple comparisons between $\log_{10}$-transformed means.

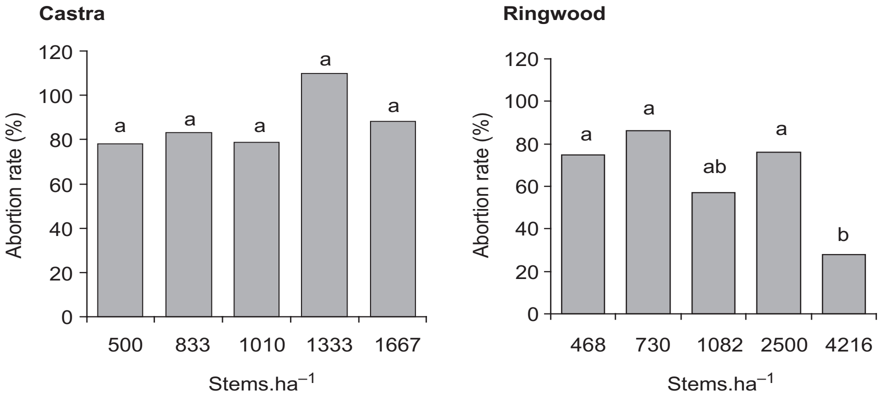

Figure 2. Abortion rate of *E. nitens* flowers that opened but were lost before maturing into capsules (100 × (aborted flowers + immature capsules) / opercula) at different planting densities in Castra and Ringwood trials. Means have been back-transformed and those with the same letter are not significantly different (P >0.05) based on Tukey–Kramer adjustment for multiple comparisons.

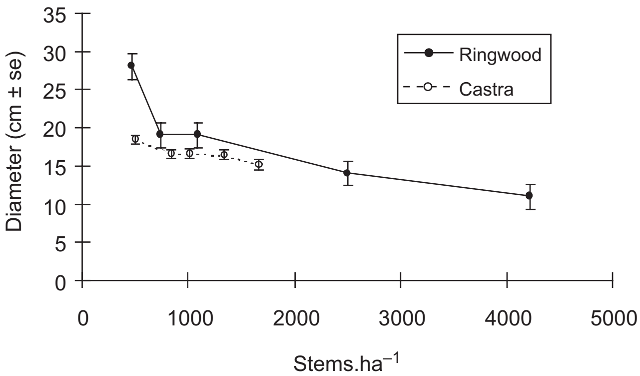

Figure 3. The diameter (± se) at breast height of *E. nitens* trees at different planting densities in two separate trials. Trees at Ringwood were measured in December 1998 when 14.5 y old whilst trees in the Castra trial were measured in May 1997 when 5 y old when the trees at closer spacing had not had as many years of intense competition as at Ringwood.

576 102 flowers ha^{-1}, respectively, for a tree density expected with a sawlog regime. This is 1.4 to 1.5 times the number of flowers per hectare expected from a pulpwood plantation respectively, a difference which increased by 8–10 times if the same calculations were undertaken using data from the 5-y-old Castra site.

The negative relationship between tree density and flower production is also expected to translate to seed capsule output. There was no significant difference in the estimated rate of flower abortion at different tree densities with the exception of the densest spacing examined (4212 stems ha^{-1} at Ringwood, Fig. 2). At this high density, flower abortion was lower than at less-dense spacings, which would slightly counter the negative trend observed for flower number. The numbers of mature capsules collected are likely to be a direct reflection of the size of the seed crop held in the tree canopies for dispersal. The fact that there is a significant positive correlation between the number of opercula per hectare and the number of mature capsules per hectare collected from the previous season's flowering (Castra $r = 0.59$, $P < 0.01$; Ringwood $r = 0.80$, $P < 0.001$) would support the hypothesis that the negative trends in reproductive output with increasing density are stable across years. Indeed, the number of mature capsules collected per tree ($F_{4,12} = 3.8$, $P < 0.05$ at Castra; $F_{4,19} = 21.2$; $P < 0.001$ at Ringwood) was significantly reduced at increased planting density. This trend was evident but not statistically significant for the number of mature capsules per hectare ($F_{4,12} = 2.09$, $P = 0.146$ at Castra; $F_{4,19} = 2.6$; $P = 0.068$ at Ringwood).

Tree dbhob significantly decreased as inter-tree spacing decreased at both Castra ($F_{4,12} = 4.06$, $P < 0.05$) and at Ringwood ($F_{4,19} = 14.9$, $P < 0.001$) (Fig. 3). However, variation in dbhob alone could not account for the effect of spacing on the number of flowers per tree at the older Ringwood site as the effect of spacing on the number of flowers remained significant ($F_{4,18} = 6.88$, $P = 0.002$) after the inclusion of dbhob as a covariate in the analysis. In contrast, at the younger and more productive Castra site, the effect of spacing on flower production was not significant ($F_{4,11} = 2.43$, $P = 0.110$) when dbhob was included as a covariate in the analysis.

Discussion

While close spacing has long been assumed to reduce flowering in eucalypt plantations, this effect has not previously been quantified. The present study shows that flower abundance in *E. nitens* increases as tree density decreases on both a per-tree and per-hectare basis, and suggests that this effect is carried through to capsule production. A similar result has also been found in other tree species such as *Clophospermum mopane* (Smit and Rethman 1998) and for cone abundance in *Abies pinsapo* (Arista and Talavera 1996). It is common for trees under strong competition for resources such as water, nutrients and light to suppress reproductive development (Jackson and Sweet 1972; Owens 1991). In the Castra trial, there was some competition at all spacings as indicated by the lifting of the green crown, the degree increasing with stocking rate (Neilsen and Gerrand 1999). This effect was also noticed at the Ringwood site during the present study. At lower stocking rates and lower levels of competition, the retention of live branches low on the stem leads to a greater volume of canopy overall (Neilsen and Gerrand 1999; Medhurst and Beadle 2001) and more meristems from which flowers develop. A deeper crown at wider spacing could account for the increase in the number of flowers per hectare even as stocking rate decreased, but the possibility of there being more flowers per unit crown volume cannot be dismissed.

The two trials studied clearly showed that there is potential for pollen and seed production in *E. nitens* pulpwood plantations (see also Moncur *et al.* 1994). The reproductive phase of *E. nite*ns plantations can commence around 4–5 y of age (Williams *et al.* 2003) and this, with results of both trials examined here, illustrates the potential for a pulp plantation to produce pollen and seeds over about two-thirds of its rotation length. Between 8735 (5-y-old site) and 234 098 (13-y-old site) flowers were produced per hectare over a single flowering season at these two study sites at the planting densities expected of a pulpwood plantation. These values relate to the level of flowering expected from the interior of a pulpwood plantation and do not account for the flowering that may be enhanced on plantation edges where crowns are deeper and exposed to more light. In addition, as site (Moncur *et al.* 1994; Williams 1999; Williams *et al.* 2003) and genetic (Dutkowski *et al.* 2001) factors are known to influence flower production in *E. nitens*, we cannot determine how much of the difference in flower production between the two study sites is due to plantation development with age as opposed to these other factors.

The increased flowering at lower tree densities observed in these two spacing trials suggests that greater flowering would be expected on a per-hectare basis under the lower density regimes used for sawlog production compared with pulpwood regimes. Sawlog production from *Eucalyptus nitens* plantations requires greater rotation lengths of typically 20–25 y (Medhurst *et al.* 2001). Consequently the reproductive phase is a much higher proportion of the rotation length, at three-quarters to four-fifths. Sawlog plantations require pruning, which typically occurs three times at annual intervals at ages of around 3–6 y, each time removing about the lower half of the live crown with the aim of eventually producing 6.4 m of clear stem (Pinkard and Beadle 1998). Through the loss of meristems, this would reduce the ability of individual trees to produce flowers. However, pruning is carried out on only one-third of the trees in a stand (Forestry Tasmania 2002), thus diluting the effect of pruning on flower production at the stand level. A more substantial effect on flower production would be anticipated when the stand is thinned at the completion of the pruning cycle, around 5–7 y of age (Pinkard and Neilsen 2003), where only 200–300 of the best pruned trees per hectare (Medhurst *et al.* 2001) are grown on for a further 18–20 y until sawlog harvest. Relatively high levels of flower production from such widely-spaced trees would be expected as this is similar to the system adopted in seed orchards where maximum flower production is desirable (Moncur 1998).

In conclusion, it is important to understand factors affecting the reproductive output of eucalypt plantations grown in Australia as there is a risk of pollen- or seed-mediated gene flow resulting in the establishment of non-native hybrids or wildlings (Barbour *et al*. 2003, 2005). The present study shows that plantation silviculture is one of the many factors that needs to be considered in quantifying this risk. Decreased spacing can significantly increase the number of flowers per tree and per hectare in *E. nitens* plantations, and it is argued that there is likely to be greater flowering, and thus pollen and seed production, per hectare from *E. nitens* plantations managed at wider spacing such as used for sawlogs as opposed to pulpwood production alone. This effect would be further exacerbated by the greater proportion of time the plantation would exist with trees in the reproductively mature phase.

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