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The impact of flower density and irrigation on capsule and seed set in *Eucalyptus globulus* seed orchards

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Abstract Low capsule set is a major factor limiting the productivity of *Eucalyptus globulus* seed orchards. This study tested the effect of flower density, as well as two common irrigation techniques on capsule and seed set. Ramets with high flower density had significantly lower capsule set (69.7%) than those with low flower density (81.7%). In a regulated deficit irrigation trial, the non-irrigated ramets set a higher proportion of capsules (63.6%) than the ramets that received conventional irrigation (CI) (51.4%). In a partial root zone drying (PRD) trial, capsule set was highest in the absence of irrigation (74.7%) followed by the PRD treatment (67.8%) and then CI (53.7%). The CI treatment tended to produce the highest number of seed per capsule. Increased water availability resulted in increased vegetative growth, which was associated with higher levels of abortion in developing capsules but those surviving tended to have higher seed set. It is argued that the observed effects of irrigation and flower density can be explained by resource competition between vegetative and reproductive growth as well as competition among reproductive structures themselves.

Keywords *Eucalyptus globulus* · Capsule set · Seed set · Reproductive success · Partial root zone drying (PRD) and regulated deficit irrigation (RDI)

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Introduction

Eucalyptus globulus (Tasmanian blue gum) is a dominant species of coastal forests in south-eastern Australia (Williams and Potts 1996), specifically in Tasmania, the Bass Strait Islands and the coastal regions of Victoria on mainland Australia (Dutkowski and Potts 1999; Jordan et al. 1993). It is the premier *Eucalyptus* species for pulpwood plantations in many temperate countries around the world including Australia, Chile, China, Columbia, Ethiopia, India, Peru, Portugal, Spain, USA and Uruguay (Eldridge et al. 1993; Potts 2004). While plantations are primarily grown for pulpwood production, there is increasing interest in their use for veneer and solid wood products (Greaves et al. 2004). Most plantations are established using seedlings from improved germplasm derived from open-pollinated seedling (Griffin 2001; Tibbits et al. 1997) or grafted (Patterson et al. 2004b) seed orchards, or through large-scale manual pollination systems (Patterson et al. 2004a). A major problem with the latter systems is that a significant proportion of hand-pollinated flowers do not set fruit (Espejo and Griffin 2001; Suitor et al. 2008). Due to the labour intensive nature of the production system, this problem can significantly increase the cost of seed production.

Little is known about the causes of capsule abortion in *E. globulus*, no doubt due to the small size and recent emergence of the industry. Capsule or fruit abortion is, however, not only an issue in *E. globulus* seed orchards; it is a widespread problem throughout horticulture and forestry (Burd 1998; Ruiz et al. 2001; Stephenson 1981). Based on what is known from studies on horticultural species, it is likely that final seed and fruit set is limited by numerous factors including resource allocation (Sedgley and Griffin 1989; Taylor and Obendorf 2001; Wesselingh 2007). Plants have limited resources available for reproduction (Wesselingh 2007), and in situations where total assimilate demand exceeds supply, fruits with the lowest sink strength are more likely to abscise (Ruiz et al. 2001). A strong sink will pull nutrients from further away than a weak sink (Wesselingh 2007). The regulation of flower and fruit numbers may be considered as an adjustment of maternal investment to match available resources (Burd 1998; Lloyd 1980; Stephenson 1981).

With the development of *E. globulus* seed orchards several management practices have been introduced to decrease tree size and enhance productivity (Potts et al. 2007). These include the use of grafted trees during orchard establishment and pruning to keep the trees at a manageable height (Sedgley and Griffin 1989). Paclobutrazol is routinely applied to provide the benefits of reduced vegetative growth (Hasan et al. 1992) permitting easier canopy management (Hetherington and Jones 1990), enhanced flowering (Griffin et al. 1993) and reduced generation times (Hasan and Reid 1995). In addition, some seed orchards are irrigated, primarily to avoid drought stress. Grafting and pruning alter the flow of resources to minimise apical dominance and keep trees in a stunted form (Cline 1991); paclobutrazol application alters the allocation of resources from vegetative to reproductive sinks through the inhibition of gibberellin synthesis (Griffin et al. 1993); but little is known about the effect of irrigation on the partitioning of resources within *E. globulus* trees. Although current practices manipulate within tree resource allocation to produce desired management outcomes, their impact on capsule set is poorly understood (Callister and Collins 2007).

Although there is little knowledge on the impact of water management on the *E. globulus* seed production system, it has been extensively studied in other horticultural species. Efficient water management is an important component of horticultural crop production not only as a means to avoid many yield and quality problems associated with exposure to water stress (Kang and Zhang 2004), but also for the positive effects associated with the control of vegetative growth and the increased production of flowers and fruit (Dry and Loveys 1998). Regulated deficit irrigation (RDI) and partial root zone drying (PRD) are the two main irrigation strategies used to restrict vegetative growth and promote reproductive growth in perennial crops (Dry and Loveys 1998).

Regulated deficit irrigation, a technique used in various horticultural species, involves restricting irrigation in order to apply a controlled drought stress. The treatment works on the premise that vegetative growth is more sensitive to water stress than fruit growth, thus calculated reductions in plant water availability result in decreases in vegetative growth and increases fruit retention (Dry and Loveys 1998). The adaptation to reduced water supply is primarily achieved through a reduction in stomatal conductance and, over the longer term, a reduction in the number of new leaves produced (Cameron et al. 2006). PRD is a relatively new irrigation technique primarily used in grapes whereby approximately half of the root mass is irrigated while the other is left dry. As a result chemical signals produced by roots exposed to drying soil prompt a physiological response in the plant which results in higher fruit retention (Davies and Zhang 1991; Dry and Loveys 1998).

While for *E. globulus* there are no management practices specifically implemented for controlling capsule set, effective strategies have been developed for other species. Therefore this study was aimed to identify the effect of resource competition on capsule set and to evaluate the potential of both RDI and PRD irrigation regimes to control shoot growth and reproductive development of grafted *E. globulus* trees in a seed orchard environment.

Materials and methods

Experimental design

Eucalyptus globulus trees used in this study were located in a seed orchard in Cambridge, south-eastern Tasmania (42°48′27.23″S 147°25′58.48″E), encompassing the Furneaux Group, Strzelecki Ranges and Western Otway races as defined by Dutkowski and Potts (1999). Cambridge has an altitude of 40 m with an annual rainfall of 507 mm and average maximum and minimum temperatures of 17.4 and 8°C, respectively. Trials were carried out over three consecutive seasons 2004/2005, 2005/2006 and 2006/2007.

2004/2005: Flower density

The influence of initial flower number per tree on capsule set was assessed in a pairwise comparison replicated 12 times. Each replicate pair consisted of ramets (clones of the same genotype) selected because of their similar size and location in the same section of the orchard. They were then pollinated with the same pollen source using the same technique [open pollination (OP) (ten pairs) or mass supplementary pollination (MSP) (two pairs)] but differed in flower density; one high and the other low in flower number per ramet. Mass supplementary pollination was achieved by cutting 1 mm off the tip of the style and applying a pollen mix (Patterson et al. 2004a). Capsule set was measured by placing two litter traps, each measuring 1,000 × 400 mm × 50 mm, underneath each ramet, one on the northern and the other on the southern side of the trunk. The number of opercula collected from the traps provided an estimate of flower number, and the number of aborted capsules collected was divided by the number of opercula as a measure of percentage capsule abortion.

2005/2006: RDI trial

Capsule set was measured in a RDI trial comprising a pairwise comparison replicated seven times. Each pair consisted of similar sized ramets located in the same section of the orchard and were open pollinated. One of the ramets received regulated deficit irrigation (RDI) while the other received the conventional irrigation (CI). Irrigation was delivered using micro-irrigators; ramets received 14 l of water in and hour three times a week for a total of 42 l of water per week. Regulated deficit irrigation was achieved by switching the irrigation off and only applying water when soil moisture reached levels at which the plants were stressed [leaf water potentials below −3.5 MPa (Bell and Williams 1997)]. The treatments commenced at the time of flowering, which for the selected genotypes mainly occurred in December but date varied due to genotypic variation (Gore and Potts 1995), and proceeded until March. Total rainfall for the duration of the trial from December to March was 144.7 mm. Soil moisture was recorded using Hansen data loggers (AM400) with sensors placed 30, 60 and 100 cm below the soil surface under each of the two ramets at each of the two locations within the orchard. Soil moisture was consistent with the treatments applied; that is, the soil was drier for the RDI treatment than the CI (data not shown). Capsule set was measured by placing litter traps under each ramet.

2006/2007: PRD trial

Capsule set was measured on three ramets of similar size, located at close proximity to each other within the orchard, all ramets different to those used for the RDI trial (replicated seven times). All selected ramets had similar flower density and were open pollinated. One of the ramets received regulated deficit irrigation (RDI) (as in the previous RDI trial), one received the conventional irrigation (CI), and the other received half conventional irrigation to one side of the ramet, with sides swapped every 2 weeks, to induce partial root zone drying (PRD). Conventional irrigation delivered approximately 42 l of water per week. PRD was applied through micro-irrigators that delivered 8 l of water per hour, and were switched on for 1 h intervals three times a week so each ramet received approximately 24 l of water per week to half its root system. The treatments were applied from December to March. Total rainfall for the duration of the trial from December to March was 193.4 mm.

Soil moisture was recorded using Hansen data loggers (AM400). One sensor was placed at 60 cm below the soil surface under each of three ramets, one from each irrigation treatment, at two locations in the orchard. These measurements revealed that CI treated ramets had more water available for the majority of the season than those that received the PRD or RDI treatments, and the PRD treated ramets had more water available for the majority of the season than those that received RDI, consistent with the amount of irrigation water applied in each treatment (data not shown). Leaf water potential measurements were made on mature leaves throughout the canopy of every ramet in the PRD trial on 2/2/2007 at regular intervals, with a pressure chamber (PMS Instrument model 615).

Vegetative growth was measured on each ramet over the 4 months period of the trial. The length of five-second order branches was measured on each ramet on the date of flowering in December. The length of the same branches was again measured at the conclusion of the trial in March. Initial branch length for each replicate within treatments was variable, which resulted in a variance between replicates for absolute increase in branch length. This problem was eliminated by converting data into the relative increase (RI) in shoot growth, by dividing the branch length at the end of the season by its length at the start of the season for each replicate. The values for each of the five branches were then averaged to give a RI in branch length per ramet.

Capsule set was calculated by placing litter traps under each ramet to record the number of opercula and aborted capsules. Flower bud numbers were recorded on each ramet immediately prior to the 2007/2008 flowering season. Seed set per capsule was measured by randomly collecting 100 capsules from each ramet at approximately 12 months after pollination, and drying them at 40°C for 48 h. Once dried, seeds were extracted and counted as viable (filled) following Hardner and Potts (1995). Seed set per capsule was only measured for five of the seven replicates for which capsule set was measured.

Statistical analysis

Differences in mean capsule set, seed set and reproductive success (seeds set per flower pollinated) between treatments for the flower density and RDI trials were assessed using a Paired Student's *t*-test. Differences in mean capsule set, seed set, seed per flower, flower buds, relative increase in vegetative growth between treatments in the PRD trial and the differences in leaf water potentials were tested by fitting a linear model with replicate and treatment as fixed effects using PROC GLM of SAS version 9.1 (SAS Institute Inc 2003). Comparisons of treatment means were then made using the Tukey–Kramer adjustment for multiple contrasts. Spearman's rank correlation coefficient (r_s) was used for all correlations.

Results

In the 2004/2005 flower density trial, ramets with a high flower density had a significantly (paired $t_{11} = 3.13$; $P < 0.01$) lower level of capsule set (67.9 ± 6.4%) than the low flower density ramets (81.7 ± 6.0%) (Fig. 2). This trend was shown for both of the two pairs which were MSP and eight of the ten pairs which were OP.

In the 2005/2006 RDI trial, percent capsule set for ramets that received the CI (51.4% ± 8.1) treatment was lower than ramets receiving RDI (63.6% ± 6.0) in the 2005/2006 RDI trial (Fig. 3), however, the differences were not statistically significant (paired $t6 = 1.53$; $P = 0.178$)".

In the 2006/2007 PRD trial the leaf water potential measurements revealed that the CI treatment consistently had the highest leaf water potential, followed by the PRD and RDI treatments (Fig. 1). Ramets that received the conventional irrigation (CI) treatment had the lowest level of capsule set (53.7% ± 9.2) followed by PRD treated ramets (67.8% ± 8.8) and ramets that received RDI (74.7% ± 7.6) (Fig. 4a). The significant differences in capsule set between irrigation treatments ($F_{2,17} = 3.95$; $P < 0.05$) were due to the significant difference between the CI and RDI treatments (Fig. 4a). The opposite response was observed for seed set (Fig. 4b). Ramets that received the CI treatment had the highest seed set (10.5 seeds per capsule ± 3.5) followed by PRD treated ramets (7.8 ± 1.8) and then ramets that received RDI (7 ± 2.0) (Fig. 4b). Although the differences in seed set ($F_{2,11} = 3.79$; $P = 0.07$) were not significant. When the contrasting responses of capsule set and seed set to irrigation were combined it resulted in no significant ($F_{2,11} = 0.07$, $P = 0.93$) differences in reproductive success (seeds obtained per flower pollinated) between any of the treatments (Fig. 4c). As flower bud initiation occurs in the season prior to anthesis (Espejo et al. 1996), it was postulated that irrigation treatments may affect

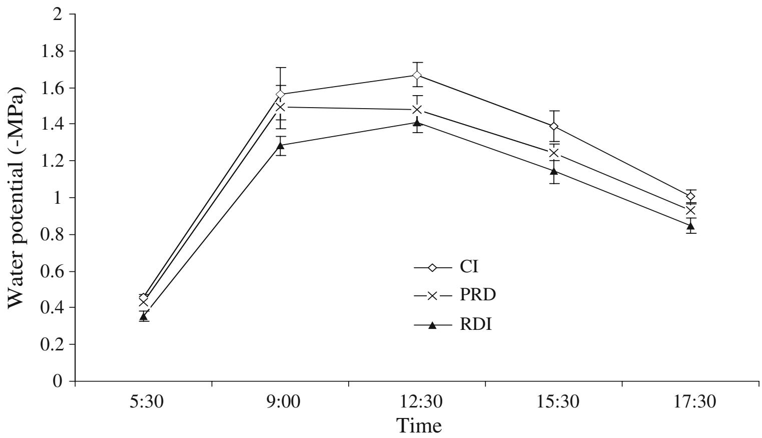


Fig. 1 Diurnal changes in leaf water potential (MPa) on 2/2/2007 for ramets that received conventional irrigation *CI*, partial root zone drying *PRD* and regulated deficit irrigation *RDI* treatments at the Cambridge site in season 2006/2007. Each point is a mean (±SE) of seven replicates. Differences were significant at 5:30am ($F_{2,17} = 5.27$; $P < 0.05$), 12:30 pm ($F_{2,17} = 2.2$; $P < 0.05$) and 5:30 pm ($F_{2,17} = 5.27$; $P < 0.05$)

Fig. 2 Mean percent capsule set (±SE) for ramets with high and low flower density at Cambridge in season 2004/2005. High flower density ramets had an average of 1,274 flowers and the low density 352. *Different letters* within the graph represent treatment means which were significantly different ($P < 0.05$) with a paired *t*-test

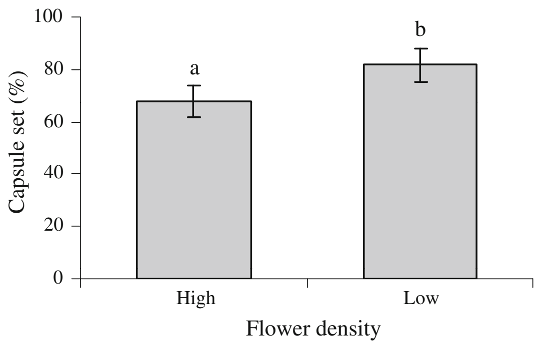
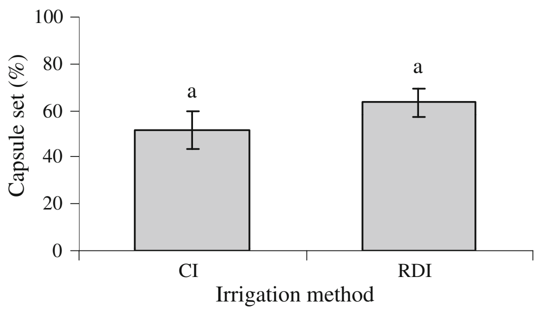


Fig. 3 Mean percent capsule set (±SE) of ramets that received conventional irrigation *CI* and regulated deficit irrigation *RDI* from flowering until the end of the capsule set period at Cambridge in season 2005/2006. *Common letters* within the graph represent treatment means which were not significantly different ($P > 0.05$) with a paired *t*-test



flower numbers in the following year. However, the number of flowers produced in the following flowering season did not significantly differ between treatments ($F_{2,17} = 0.92$; $P = 0.43$).

The relative increase in shoot length differed between the three irrigation treatments (Fig. 4d) ($F_{2,17} = 3.94$, $P < 0.05$). The CI (3.26 ± 0.37) treatment had a significantly greater relative increase in shoot length compared to RDI (2.95 ± 0.23), while the PRD (2.28 ± 0.37) intermediate did not significantly differ from the other treatment. Ramets with more water applied had increased vegetative growth, lower capsule set and a higher seed set.

Discussion

Competition for resources amongst reproductive sinks has been widely reported for species with fleshy fruits (Bawa and Webb 1984; Burd 1998; Ruiz et al. 2001; Wesselingh 2007). Resource competition between reproductive sinks for species with woody capsules has received far less attention. In a review of flower and fruit abortion, Stephenson (1981) concluded that the proportion of pollinated flowers that set fruit decreased as the total number of pollinated flowers on a tree increased. In this study the phenomenon has also been observed in *Eucalyptus globulus* seed orchards, indicating that the theories reported in the literature for fleshy fruits (Wardlaw 1990; Wesselingh 2007) may be extended to woody fruit. The results for *E. globulus* suggest that inter-capsule competition for resources exists between capsules after pollination even though the increase in capsule size, and thus relative maternal investment required, from flower pollination to capsule

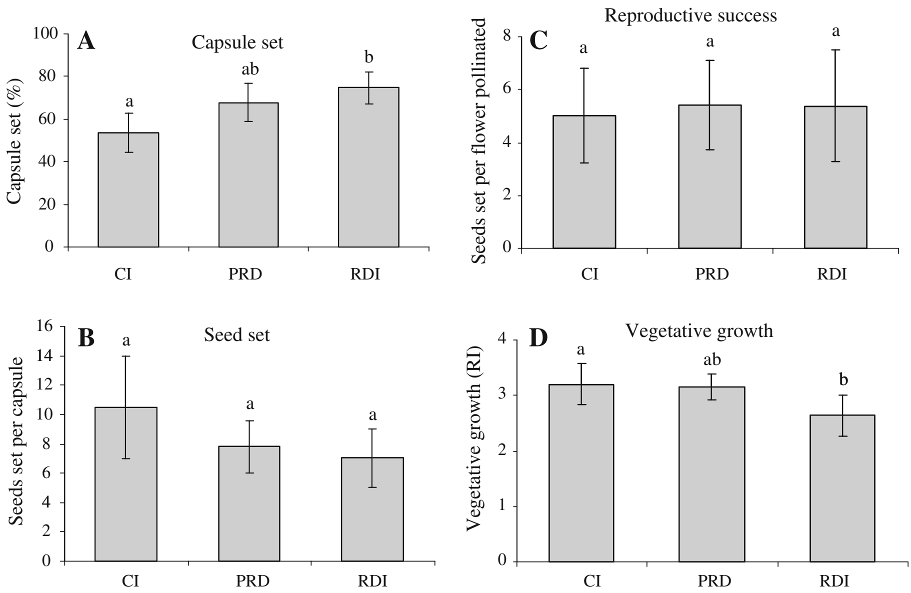


Fig. 4 Mean percent capsule set (±SE) (**a**), the number of seed set per capsule harvested (±SE) (**b**), reproductive success (±SE), as measured by seeds obtained per flower pollinated (**c**) and the relative increase *RI* in vegetative growth from flowering until end of the capsule set period (±SE) (**d**) for open pollinated ramets that received conventional irrigation *CI*, partial root zone drying *PRD* and regulated deficit irrigation *RDI* in the PRD trial (season 2006/2007). Common letters within the graphs represent treatment means that were not significantly ($P > 0.05$) different with the SSSS–Kramer method for arcsine square root transformed data (**a**) and square root transformed data (**b**, **c** and **d**)

harvest is relatively small (Suitor et al. 2008) in comparison with fleshy fruit. Most of the high and low flowering pairs tested were open-pollinated, and thus we cannot completely dismiss the possibility that the differences in capsule abortion between trees of the same genotype is due to differences in pollination success rather than resource competition. However, this is unlikely as, firstly, the same trend was observed for OP and MSP pairs, and secondly, Patterson et al. (2004a, b) showed no consistent difference in outcrossing rates between comparable high and low flower density *E. globulus* trees growing in a seed orchard.

In the present study increasing water availability through irrigation increased vegetative growth of *E. globulus* but decreased capsule set. This effect is consistent with the theory that reproductive structures not only compete with each other for the limited pool of resources within the tree, but competition exists between reproductive and vegetative sinks (Quinlan and Preston 1968; Stephenson 1981; Wardlaw 1990). Many tree species produce flushes of vegetative growth that coincide with the period of fruit development. The young expanding leaves are not net producers of photosynthates and thus are in direct competition with the developing fruits (Sedgley and Griffin 1989). Furthermore, it appears that the competition was influenced by irrigation, with conventional irrigation management promoting vegetative growth at the expense of capsule retention. The higher capsule set within the reduced irrigation treatments was consistent with the theory put forward by Hardie and Martin (1990) that vegetative growth is more sensitive to water stress than fruit growth.

Although a reduction in irrigation reduced vegetative growth and increased capsule set, it was found to have an adverse effect on seed set per capsule. While there was a slight trend for increased seed set per flower under reduced irrigation, the opposing responses of capsule set and seed set per capsule to irrigation treatments resulted in the irrigation having no statistically significant effect on overall reproductive success with the sample sizes studied. However, it is possible larger industry scale experiments would detect significant increases in total reproductive success under reduced irrigation, although the effect is likely to be relatively small in magnitude.

The increased average number of seeds set per capsule in the conventionally irrigated treatments is likely to be a direct effect of capsule abortion. *Eucalyptus globulus* capsules with the lowest seed number abort first (Suitor et al. 2008), and thus with higher capsule abortion the mean number of seed per capsule in the surviving capsules would be expected to also be higher. Nevertheless, the possibility that the drier treatments directly result in high seed abortion cannot be dismissed. Water stress has been shown to increase seed abortion in other species including maize (Boyer and Westgate 2004), lupins (Palta and Ludwig 1997) and peas (Ney et al. 1994). However, due to the size of *E. globulus* seed, its water requirements are likely to be a lot less than that of these examples and possibly still less than that of vegetative growth. Therefore the abortion of the capsules with the lowest seed number is the most plausible explanation for the inverse relationship observed between capsule and seed set.

Partial root zone drying imposed by alternating the position of the micro-irrigation from one side of the *E. globulus* trees to the other every 2 weeks, had no greater effect than the reduced level of irrigation imposed by the treatments. The level of vegetative growth and capsule set for the PRD treatment fell between the CI and RDI treatments, suggesting in this case that the benefits of the PRD treatment recorded for grapes (Dry and Loveys 1998) may not be applicable to *E. globulus*. However, the responses observed in this study to just the reduction in irrigation in both the PRD and RDI trials were similar to those of commercial horticultural species. Regulated deficit irrigation has been used successfully with pome and stone fruit, both experimentally (Chalmers et al. 1981; Mitchell et al. 1989) and commercially (Mitchell and Goodwin 1996), to reduce vegetative growth, increase fruit yield and decrease the total amount of irrigation applied over a season. Regulated deficit irrigation has also been shown to curb excessive vegetative growth in many species by reducing the internode length, making for a more compact plant (Cameron et al. 2006; Romero et al. 2004). Sedgley and Griffin (1989) have stated that "fruit set may be increased by controlling irrigation so as to reduce vegetative shoot growth immediately after flowering". It is widely accepted that vegetative and reproductive sinks compete for a limited pool of resource and in many instances fruit and seed growth dominates the growth of vegetative tissues (Wardlaw 1990). This is certainly consistent with results for eucalypts, where water-stressed plants of *E. globulus* produced fewer lateral branches, allocating less biomass to branches than well-watered plants (Osorio et al. 1998). Within other *Eucalyptus* species vegetative growth has been shown to be delayed and/or reduced by developing flowering buds (Pook 1984) and prolific flowering years have resulted in reduced leaf production compared with non-flowering years (Abbott and Loneragan 1986). Although RDI has been shown to reduce vegetative growth and enhance fruit set in numerous species and now eucalypts, there are no detailed studies to date outlining the impact of RDI on overall seed production for any species.

In summary, in the commercial *E. globulus* seed orchard studied, our results argue that competition for resources existed both within and between reproductive and vegetative structures. A reduction in soil water availability altered the partitioning of resources to increase capsule set and reduce vegetative growth. Therefore this study demonstrates that the orchard management technique of RDI effectively applied in other species is transferable to the *E. globulus* production system. However, while increased capsule set under reduced irrigation was observed, which is the response required in the horticultural industry where fruit is the product, the reduction in seed set per capsule appears to counter this positive effect for a system where seed production is the overall objective. While no direct recommendations in terms of identifying optimal irrigation levels to maximise seed output can be made, this study has shown that *E. globulus* reproduction is sensitive and responsive to plant water availability, and has highlighted the complex interactions which occur between vegetative and reproductive growth as well as amongst the various components driving reproductive success in this species.

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