**CSIRO** PUBLISHING
www.publish.csiro.au/journals/ajb *Australian Journal of Botany*, 2005, **53**, 251–257

# Water and nutrient availabilities do not affect lignotuber growth and sprouting ability of three eucalypt species of south-eastern Queensland

*Judi R. Walters*[A], *Alan P. N. House*[A,B,D] *and David Doley*[C]

[A]Queensland Forestry Research Institute, Fraser Road, Gympie, Qld 4570, Australia.
[B]Current address: CSIRO Sustainable Ecosystems, Queensland Bioscience Precinct, 306 Carmody Road, St Lucia, Qld 4067, Australia.
[C]Department of Botany, University of Queensland, St Lucia, Qld 4072, Australia.
[D]Corresponding author. Email: alan.house@csiro.au

*Abstract.* Shoot biomass and lignotuber size of seedlings of three eucalypt species, *Eucalyptus acmenoides* Schauer, *E. siderophloia* Benth. and *Corymbia variegata* [syn. *E. maculata* (F.Muell.) K.D.Hill and L.A.S.Johnson], were measured for glasshouse-grown seedlings established under two water and nutrient regimes. Seedlings were subjected to shoot removal (clipping) at ages from 9 to 19 weeks, and transferred to the high water treatment for a further 8 weeks to assess shoot emergence from lignotubers. Seedling shoot biomass was greater in both the high than the low nutrient and water treatments, but lignotuber diameter was not affected significantly. *C. variegata* seedlings had the largest lignotuber diameters, followed by *E. siderophloia* and *E. acmenoides*, respectively. Although growth of shoots was influenced by nutrient availability, results suggest that species differences in the growth of lignotubers was less affected. It is suggested that lignotuber growth was strongly influenced by genotype. More than 70% of *C. variegata* seedlings clipped at 9 weeks sprouted, compared with only 5 and 10% of seedlings of *E. siderophloia* and *E. acmenoides*, respectively. All *C. variegata* seedlings sprouted after being clipped at 19 weeks, but <80% of *E. siderophloia* and <60% of *E. acmenoides* sprouted when clipped at the same age. It was concluded that seedlings forming part of the regeneration stratum in dry sclerophyll forests need to be protected from damage for at least 4 months (for *C. variegata*) or at least 6 months (for *E. siderophloia* and *E. acmenoides*) if they are to survive by sprouting from lignotubers.

## Introduction

Seedling regeneration of eucalypt species in the dry sclerophyll forests of south-eastern Queensland derives primarily from seedlings with lignotubers (lignotuberous seedlings). Lignotubers are basal, woody swellings that contain buds from which new stems arise after damage to the aerial portion of a plant (Jacobs 1951; James 1984). Lignotubers also contain non-structural carbohydrates, which are used to support sprouting (Canadell and Lopez-Soria 1998). Lignotubers can form within a few weeks of seed germination in eucalypt species (Kerr 1925; Graham *et al.* 1998) and their development is thought to be influenced by environmental conditions, especially the availability of water and nutrients, although the magnitude and direction of effects may depend on species and levels of treatments applied (Beadle 1968; Mullette and Bamber 1978; Jahnke 1983). Lignotuber growth is generally believed to be enhanced by conditions that promote plant growth (Kerr 1925; Fordyce *et al.* 1997), larger seedlings having larger lignotubers. However, the effects of environmental conditions on relative allocation of biomass to lignotubers have not been reported. Indeed, allocation to roots and underground or basal organs, such as lignotubers, relative to shoots, may be increased when water and nutrients are deficient (Ingestad and Agren 1991; Kozlowski and Pallardy 1997). Whether or not a species develops lignotubers is genetically controlled (Pryor 1957) and in some species, allocation to lignotuber development is influenced by genotype (Walters *et al.* 2005).

The effects of environmental conditions on lignotuber growth may be important because not all lignotuberous seedlings have the ability to survive removal of aerial parts (Florence 1996) and lignotuber size is thought to influence the ability of a lignotuber to sprout after removal of the aerial portion of a lignotuberous seedling. Within some species, plants with larger lignotubers have been found more likely to survive damage than plants with smaller lignotubers (Jahnke 1983; Auld 1990). Fordyce *et al.* (2000) hypothesised that the critical difference between *Allosyncarpia ternata* S.T.Blake seedlings that are able to sprout and survive after damage by fire and those not able to sprout is lignotuber size. However, in a glasshouse study, *E. maculata* seedlings that had small lignotubers because they were grown in dry soil produced

10.1071/BT04021 0067-1924/05/030251

more sprouts when they were clipped and given an oversupply of water and nutrients than did seedlings with larger lignotubers that had been grown in well watered soil (Neave and Florence 1998). This finding suggests that the sprouting ability of seedling lignotubers may be determined by the conditions under which the seedling becomes established rather than the size of the lignotuber.

Within the eucalypts, lignotuberous seedlings of different species can show differing rates of recovery following disturbance by fire (Noble 1984). This leads to questions about the effects of such difference on the regeneration of native mixed-species forests in Australia. Differences in the sprouting and survival ability of eucalypt species and the influence of environmental factors such as soil moisture and nutrient availability may result in the need for specific management guidelines to promote and protect seedling regeneration in these forests.

The species composition of native dry sclerophyll forests of south eastern Queensland varies across the distributional range of the forests but in many areas is dominated by three eucalypt species: *E. acmenoides*, *E. siderophloia* and *C. variegata* (Henry and Florence 1966; Florence 1996). Seedlings of these three species all develop lignotubers and a store (pool) of lignotuberous seedlings often exists under the forest canopy. Seedlings of *C. variegata* are able to grow directly into small trees without an intermediate 'lignotuberous' stage (Forestry Commission of New South Wales 1985); however, such growth is usually the result of uncommonly favourable conditions, including the absence of prolonged drought, destructive grazing or fire. As such, seedlings of the three species can persist for a number of years after establishment under the forest canopy in a suppressed, largely prostrate state (Jacobs 1951; Henry and Florence 1966). Seedlings of *E. acmenoides* and *E. siderophloia* generally exhibit growth dynamics similar to those of *C. variegata*, although species differ in rates of establishment, survival and growth under a forest canopy. Therefore, the relative tolerances of species to various environmental conditions may be important in determining the growth and distribution of seedling regeneration in mixed-species forests.

The aim of this study was to determine the effects of soil moisture and nutrient availabilities on the size of lignotubers in three eucalypt species, and further, to test the hypothesis that seedlings with larger lignotubers are better able to survive by sprouting after removal of shoots than seedlings with smaller lignotubers.

## Materials and methods

Seed of *Eucalyptus acmenoides* Schauer, *E. siderophloia* Benth. and *Corymbia variegata* [syn. *E. maculata* (F.Muell) K.D.Hill and L.A.S.Johnson] was collected from 4–6 parent trees within an area (approximately 1 km radius) in the Maryborough State Forest and sown directly into pots containing a pine bark and vermiculite potting medium, with either a high nutrient (HN) level [5–6-month release Osmocote (Scotts-Sierra Horticultural Products, Marysville, OH) at a rate of 3.5 g $L^{-1}$ of potting mix] or a low nutrient (LN) level (Osmocote at 0.5 g $L^{-1}$). A total of 144 plants were raised, half being HN and the other half being LN. Pots were arranged in two separate randomised blocks in the glasshouse, one block on each of the two benches used. In the glasshouse, day-time (0700–1900 hours) temperatures were maintained between 15 and 38°C and night-time temperatures were maintained between 5 and 15°C. Pots were watered for 7 weeks by an overhead watering system; germinants were thinned to one plant per pot after 3 weeks. After 7 weeks, watering treatments were commenced. Seedlings on one bench constituted the high water (HW) treatment, receiving water four times in each 24-h period, such that the potting mixture was maintained near field capacity. Seedlings on the other bench made up the low water (LW) treatment and were watered when leaves showed signs of severe wilting but before damage resulted in plant death, the amount of water given governed by the size of individual plants. In general, seedlings in the low water treatment with high nutrients were watered every second day and seedlings in the low water treatment with low nutrients were watered every third day.

At 2-week intervals, beginning 9 weeks after seeds were sown (2 weeks after initiation of water treatments), six seedlings of each species were selected from each water–nutrient treatment combination. Net lignotuber diameter was measured for selected seedlings by subtracting the diameter of the stem just above the lignotuber from the maximum lignotuber diameter and shoot biomass was determined after clipping seedling stems 5 mm above the lignotuber and drying at 80°C for 48 h.

The lignotubers and roots in pots were kept in the glasshouse for 8 weeks after removal of the shoots and the number of seedling lignotubers that produced sprouts that were still alive at the end of the 8-week period was recorded as 'survived' and those that produced sprouts but were dead at the end of the 8-week period were 'sprouted but dead'. During the 8 weeks after clipping, the potting mixture of seedling lignotubers in the HW treatment was maintained near field capacity by watering once every day and the potting mixture of seedling lignotubers in the LW treatment was watered once every 4 days.

### *Statistical analyses*

Shoot biomass and lignotuber diameter data were analysed by two-way ANOVAs, where both nutrient and water treatments were fixed factors. Student's *t*-tests were used to analyse differences in measured parameters among treatments within species at each measurement date. Analyses were performed with MINITAB for Windows: differences of $P < 0.05$ were considered significant for all tests.

## Results

Shoot biomass of seedlings of all three species was approximately three times greater in the HN than in the LN treatment (Fig. 1). In the HN treatment, HW seedlings had greater shoot biomass than LW seedlings at Week 19. However, the difference was not significant ($P = 0.07$). There was no significant interaction between the water and nutrient treatments. There were significant differences in shoot biomass among species; shoot biomass of *C. variegata* was nearly twice that of the other two species after 19 weeks. This difference was significant at Week 17 in both HN and LN treatments ($P = 0.03$).

The two factors that most influenced lignotuber size were seedling age and species. Older seedlings generally had larger lignotubers than did younger seedlings and the lignotuber diameter of *C. variegata* seedlings was consistently twice that of the seedlings of the other two species at the same age. Neither the water nor nutrient treatments had statistically significant effects on the net lignotuber diameter of seedlings (Fig. 2), although HN seedlings generally had larger lignotubers than LN seedlings. *C. variegata* always had the largest lignotubers, the difference being significant from the commencement of measurements (Week 9). This species also had greater variation in lignotuber growth among treatments than did the other two species, although these differences were not statistically significant. The mean net lignotuber diameter of *C. variegata* seedlings clipped at Week 9 was 2.4 mm, twice that of *E. acmenoides*, and the proportions of seedling lignotubers of these two species that sprouted were approximately 0.7 and 0.1, respectively. At Week 17, when the mean lignotuber diameter of each of the two *Eucalyptus* species was similar in size to that of 9-week-old *C. variegata* (i.e. 2.4 mm), the proportion of seedling lignotubers that sprouted was approximately 0.6.

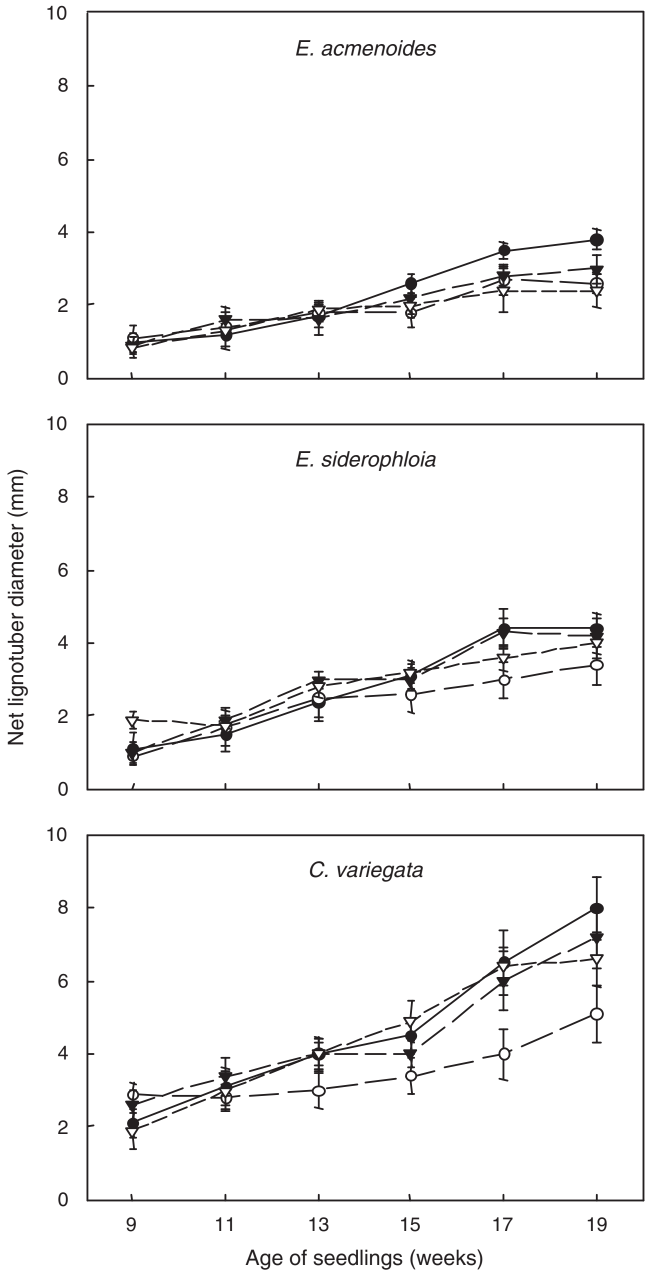

**Fig. 1.** Mean shoot biomass of glasshouse-grown *Eucalyptus acmenoides*, *E. siderophlia* and *Corymbia variegata* seedlings from 9 to 19 weeks of age under two water and two nutrient treatments: ●, high water, high nutrients; ○, low water, high nutrients; ▼, high water, low nutrients; ▽, low water, low nutrients.

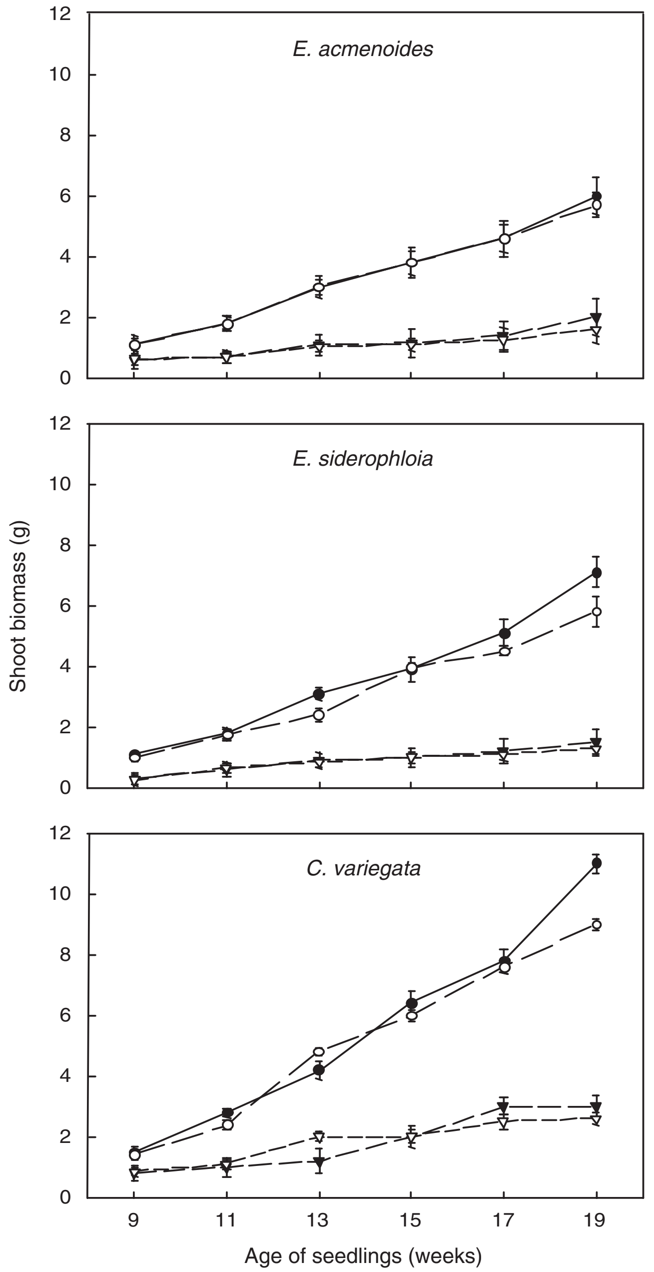

**Fig. 2.** Mean net lignotuber diameter of glasshouse-grown *Eucalyptus acmenoides*, *E. siderophlia* and *Corymbia variegata* seedlings from 9 to 19 weeks of age under two water and two nutrient treatments: ●, high water, high nutrients; ○, low water, high nutrients; ▼, high water, low nutrients; ▽, low water, low nutrients.

Nutrient treatments produced significant differences in allocation of growth between shoot biomass and lignotubers. LN seedlings allocated a greater proportion of growth resources to lignotubers than did HN seedlings (Fig. 3). The ratio of shoot biomass : lignotuber diameter remained relatively constant throughout the experimental period. The difference in allocation was greatest in *E. siderophloia*, in which the ratio of biomass : lignotuber in LN seedlings was 3-fold greater than that in HN seedlings.

Figure 3 shows that the biomass : lignotuber ratio of seedlings of each species within each nutrient treatment remained relatively constant throughout the experiment, indicating no significant effect of age on the proportion of growth allocation directed towards lignotubers. In all species, LN seedlings allocated significantly more growth to lignotubers than did HN seedlings, this being most pronounced in *E. siderophloia*. The biomass : lignotuber ratios of *E. siderophloia* and *C. variegata* seedlings were similar in both HN and LN treatments (3 and 1, respectively). The ratio for HN *E. acmenoides* seedlings was similar to that of the other two species (approximately 1), the ratio

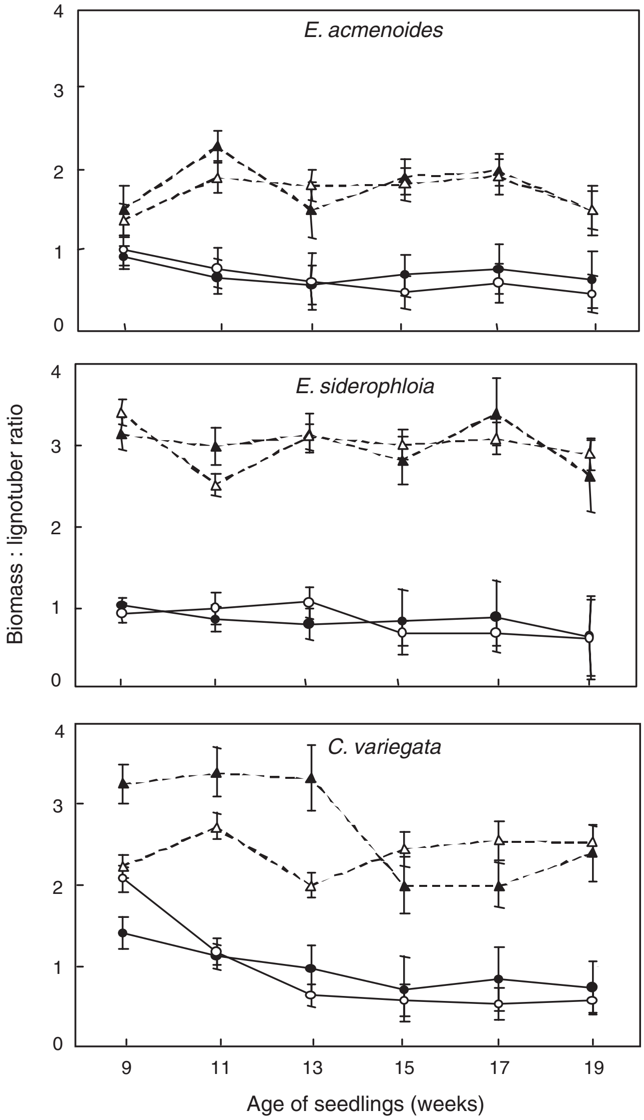

**Fig. 3.** Biomass : lignotuber ratio of *Eucalyptus acmenoides*, *E. siderophlia* and *Corymbia variegata* seedlings from 9 to 19 weeks under two water and two nutrient treatments: ●, high water, high nutrients; ○, low water, high nutrients; ▲, high water, low nutrients; △, low water, low nutrients.

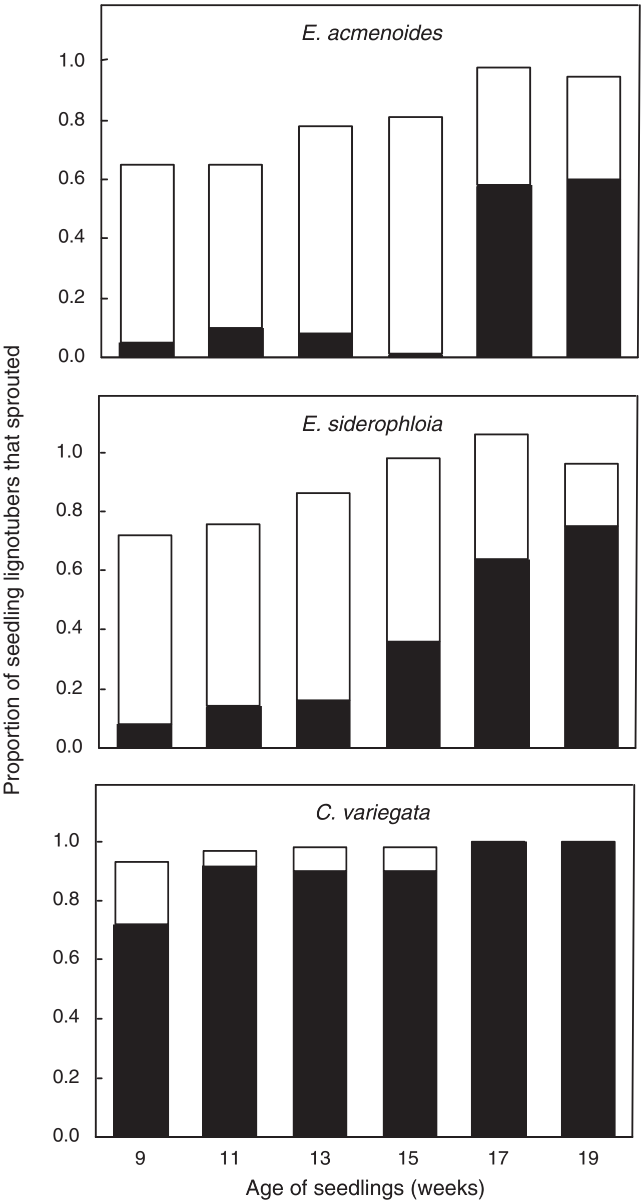

**Fig. 4.** Proportion of seedling lignotubers of *Eucalyptus acmenoides*, *E. siderophlia* and *Corymbia variegata* that sprouted within 8 weeks of clipping treatment but for which sprouts died within that period (open sections of vertical bars), and of those that sprouted within 8 weeks of clipping treatment and survived (had living sprouts) at the end of that time (shaded sections of vertical bars).

of LN *E. acmenoides* seedlings was only 2/3 of those of *E. siderophloia* or *C. variegata* (2 compared with 3, respectively).

More than 70% of *C. variegata* seedling lignotubers produced sprouts that survived the 8 weeks after the first clipping (at 9 weeks, Fig. 4). Conversely, <10% of *E. siderophloia* and <5% of *E. acmenoides* seedling lignotubers survived after the first clipping (Fig. 4). In all species, all lignotubers that sprouted did so within the first 4 weeks of the clipping event. A large proportion of seedling lignotubers produced sprouts; however, these died within a few days of appearance and no live sprouts were present after 8 weeks. The proportion of seedlings that survived after clipping generally increased with seedling age at the time of clipping; *C. variegata* always had the greatest number of sprouting seedlings, followed by *E. siderophloia*, and *E. acmenoides* always had the fewest. After the final clipping treatment (at 19 weeks), all *C. variegata* seedling lignotubers and over 70% of *E. siderophloia* and 55% of *E. acmenoides* lignotubers had sprouted and survived. There was no significant ($P = 0.34$) difference in the proportions of seedling lignotubers that sprouted between HN and LN or HW and LW treatments.

## Discussion

Growth responses of the seedlings to water and nutrient treatments varied among species and with the plant attribute measured. The lack of a measurable effect of water treatments was unusual. It is likely that the nutrient treatments had a confounding effect on watering treatments (i.e. increased growth because greater nutrient availability led to increased water use and, hence, increased water demand), since application of more water to HN seedlings than to LN seedlings was necessary to avoid significant seedling deaths through desiccation. The lack of water-treatment effects suggests that growth of all plants may have been water-limited to some degree, and it was not until the later stages of the experimental period that more pronounced water limitation produced a measurable difference between HN and LN seedlings.

Results showed that HN seedlings had greater shoot biomass than LN seedlings, and since the nutrient levels were sufficient to produce measurable responses in shoot biomass, they were expected to produce measurable differences in lignotuber growth. However, in absolute measurement terms, lignotuber growth was not significantly influenced by the nutrient treatments.

In contrast, nutrient treatments significantly influenced the proportional allocation of growth within seedlings. The ratio of shoot biomass : lignotuber diameter was higher for LN than HN seedlings, indicating that under nutrient stress, seedlings allocated a greater proportion of growth towards lignotubers. This pattern was consistent in all three species examined, being strongest in *E. siderophloia* and weakest in *E. acmenoides*. This may be a reflection of the differences in climates in the natural distributions of the species. This may be a reflection of the ecological differences over the natural distributions of these species. The natural distribution of *E. siderophloia* is greater than that of *E. acmenoides*, resulting in a more varied edaphic and climatic environment. This, in turn, can be related to greater genetic variation, allowing the species to exist in a range of environments. The greater variation in biomass allocation pattern in *E. siderophloia* may be the result of such genetic diversity.

Lignotuber growth appeared to be strongly influenced by genotype (species), with *C. variegata* seedlings having much larger lignotubers than the other two species. Seeds used in this study were likely to have limited genetic variability since, for each species, seeds were collected from no more than six parent trees within a small area in the same forest. Therefore, results from this study are representative only of trees growing in the location from which the seed was collected. However, inter-genotypic (intra-specific) variation may produce variation in lignotuber size across the geographic range of each species. Intra-specific variation in lignotuber size has been documented in *E. obliqua* (Green 1971; Brown *et al*. 1976), *E. viminalis* (Ladiges and Ashton 1974; Anderson and Ladiges 1978), *E. camaldulensis* (Karschon 1971), *C. variegata* (Henry and Florence 1966) and *E. obliqua* (Walters *et al.* 2005). The results of the present study may not be representative for the species across their entire distributional range and further experimentation is required to test the hypotheses for other provenances.

Seedlings with larger lignotubers were better able to survive by sprouting after removal of shoot biomass than were seedlings with smaller lignotubers. This was shown both as the difference in the proportion of surviving lignotubers among species and as the increase in the proportion of seedling lignotubers of each species that survived with time (age of plants). Lignotubers larger than about 2.5 mm in diameter had a markedly higher survival rate through sprouting than those smaller than 2.5 mm. Thus, there appeared to be a minimum threshold size that lignotubers had to reach before they were able to survive by sprouting. A link between lignotuber size and survival has been shown in juvenile plants of the closely related species *Angophora hispida*, where only plants with lignotubers greater than 5000 mm$^3$ in volume survived fire (Auld 1990). Similarly, Fordyce *et al.* (2000) showed that greater survival rates of *Allosyncarpia ternata* seedlings were linked with lignotuber size, and suggested that the starch-storing capacity of lignotubers determines the difference between seedlings able to survive serious damage and those unable to survive.

In the present study, the high proportion of lignotubers that sprouted but did not survive the 8-week observation period suggests that the production of sprouts was not limited by buds or meristematic factors, but rather, by some factor that became limiting to growth during the early stage of sprouting. We suggest that carbohydrate stores became limiting in this study, in a way similar to that reported by Bell and Pate (1996), where basal sprouting after clipping was limited by the amount of starch reserves held in roots of *Conostephium pendulum*. Similarly, Walters *et al.* (2005) showed that the sprouting ability of young *E. obliqua* lignotubers was closely linked with carbohydrate reserves in roots and lignotubers, rather than with meristematic limitations.

Given that age is an important factor in determining whether or not seedling lignotubers of *C. variegata*, *E. acmenoides* and *E. siderophloia* can survive damage by sprouting, there is a need for a period of protection of new germinants in a forest situation. Seedlings need to be protected from damaging agents, principally fire and grazing, until they are large enough to survive defoliation. Fire is used to control weed growth in native dry sclerophyll forests of south-eastern Queensland, so the effects of different burning frequencies on the survival of new germinants should be investigated. Henry (1961) noted that seedlings in these forests did not have a chance to recover under a regime of annual burning, although *C. variegata* seedlings are less sensitive to fire after the early stages of establishment (Henry and Florence 1966). The ability of other tree species that grow with *C. variegata*, including *E. acmenoides* and *E. siderophloia*, to recover after fire has not been reported, but differences were detected among species in this study and it is likely that different periods of protection may be required. In forest areas where more than one species is growing, a longer protection period should be used. For example, if seedling growth in the glasshouse is taken as approximation of growth in the field, *Corymbia variegata* appears to require approximately 4 months to develop lignotubers that promote survival through sprouting, whereas the two *Eucalyptus* species require a longer period of approximately 6 months. However, growth rates are likely to differ substantially between glasshouse and the forest situation; therefore, field studies are needed to determine appropriate periods of protection for the native forest environments where these species grow. There is likely to be a considerable level of variation in establishment and growth rates in a forest situation, and hence, greater variation in the period of time needed for protection of regeneration. Moreover, the effects of damage on more established seedlings in these species warrants investigation so that the disadvantages of damage by fire can be adequately weighed against the advantages of weed control. Regeneration of the dry sclerophyll forests of south-eastern Queensland depends largely on establishment and survival of seedlings with lignotubers. Without proper protection during the early stages of development, regeneration and forest health are being placed at risk.

## Acknowledgments

This work was conducted while J.R. Walters (nee Buckmaster) was supported by an Australian Postgraduate Award at The University of Queensland. The seed used was provided by the DPI Forestry Tree Seed Centre and glasshouse facilities were provided by the Queensland Forest Research Institute, Gympie. The help of the glasshouse manager, Mr Bob Scott, is gratefully acknowledged.

## References

Anderson CA, Ladiges PY (1978) A comparison of three populations of *Eucalyptus obliqua* L'Herit. growing on acid and calcareous soils in southern Victoria. *Australian Journal of Botany* **26**, 93–109.

Auld TD (1990) The survival of juvenile plants of the resprouting shrub *Angophora hispida* (Myrtaceae) after a simulated low-intensity fire. *Australian Journal of Botany* **38**, 255–260.

Beadle NCW (1968) Some aspects of the ecology and physiology of Australian xeromorphic plants. *Australian Journal of Science* **30**, 348–355.

Bell TL, Pate JS (1996) Growth and fire response of selected Epacridaceae of south-western Australia. *Australian Journal of Botany* **44**, 509–526.

Brown AG, Eldridge KG, Green JW, Matheson AC (1976) Genetic variation of *Eucalyptus obliqua* in field trials. *New Phytologist* **77**, 193–203.

Canadell J, Lopez-Soria L (1998) Lignotuber reserves support regrowth following clipping of two Mediterranean shrubs. *Functional Ecology* **12**, 31–38. doi: 10.1046/j.1365-2435.1998.00154.x

Florence RG (1996) 'Ecology and silviculture of eucalypt forests.' (CSIRO Publishing: Melbourne)

Fordyce IR, Eamus D, Duff GA, Williams RJ (1997) The role of seedling age and size in the recovery of *Allosyncarpia ternata* following fire. *Australian Journal of Ecology* **22**, 262–269.

Fordyce IR, Eamus D, Duff DG (2000) Episodic seedling growth in *Allosyncarpia ternata*, a lignotuberous, monsoon rainforest tree in northern Australia. *Austral Ecology* **25**, 25–35. doi: 10.1046/j.1442-9993.2000.01029.x

Forestry Commission of New South Wales (1985) 'Notes on the silviculture of major NSW forest types. No. 6: spotted gum types.' (Forestry Commission of New South Wales: Sydney)

Graham AW, Wallwork MA, Sedgley M (1998) Lignotuber bud development in *Eucalyptus cinerea* (F.Muell. ex Benth). *International Journal of Plant Sciences* **159**, 979–988. doi: 10.1086/297618

Green JW (1971) Variation in *Eucalyptus obliqua* L'Herit. *New Phytologist* **70**, 897–909.

Henry NB (1961) 'Complete protection versus prescribed burning in the Maryborough hardwoods.' Queensland Forestry Service Research Note No. 13.

Henry NB, Florence RG (1966) Establishment and development of regeneration in spotted gum–ironbark forests. *Australian Forestry* **30**, 304–316.

Ingestad T, Agren GI (1991) The influence of plant nutrition on biomass allocation. *Ecological Applications* **1**, 168–174.

Jacobs MR (1951) The growth and regeneration of eucalypts. *Journal of Australian Institute of Agricultural Sciences* **17**, 174–183.

Jahnke RS (1983) Studies on the eucalypt lignotuber. MSc Thesis, The Australian National University, Canberra.

James S (1984) Lignotubers and burls—their structure, function and ecological significance in Mediterranean ecosystems. *Botanical Review* **50**, 225–266.

Karschon R (1971) Lignotuber occurrence in *Eucalyptus camaldulensis* Dehn. and its phylogenetic significance. *Flora* **160**, 495–510.

Kerr LR (1925) The lignotubers of eucalypt seedlings. *Proceedings of the Royal Society of Victoria* **37**, 79–97.

Kozlowski TT, Pallardy SG (1997) 'Physiology of woody plants.' (Academic Press: New York)

Ladiges PY, Ashton DH (1974) Variation in some central Victorian populations of *Eucalyptus viminalis* Labill. *Australian Journal of Botany* **22**, 81–102.

Mullette KJ, Bamber RK (1978) Studies on the lignotubers of *Eucalyptus gummifera* (Gaertn. and Hochr.) III. Inheritance and chemical composition. *Australian Journal of Botany* **26**, 23–28.

Neave IA, Florence RG (1998) Moisture stress stimulates the subsequent growth of lignotuberous *Eucalyptus maculata* seedlings. *Australian Forestry* **61**, 114–119.

Noble IR (1984) Mortality of lignotuberous seedlings of *Eucalyptus* species after an intense fire in montane forest. *Australian Journal of Ecology* **9**, 47–50.

Pryor LD (1957) The inheritance of some characters in *Eucalyptus. Proceedlings of the Linnean Society of New South Wales* **82**, 147–155.

Walters JR, Bell TL, Read S (2005) Intra-specific variation in *Eucalyptus obliqua* seedlings. *Australian Journal of Botany* **53**, 195–203.

Manuscript received 1 February 2004, accepted 14 December 2004