

Establishment and growth of sandalwood (*Santalum spicatum*) in south-western Australia: *Acacia* host trials

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Summary

The influence of four different *Acacia* species (*Acacia acuminata*, *A. saligna*, *A. microbotrya* and *A. hemiteles*) on establishment and growth of sandalwood (*Santalum spicatum*) was examined at two sites in the wheatbelt. The host seedlings were planted in June 1998, and four *S. spicatum* seeds were planted adjacent to each host at age 1 y (May 1999). Direct seeding *S. spicatum* near 1-y-old host seedlings again proved to be a successful establishment technique, with 81–91% germination per spot, at both sites. At age 3 y, survival of *S. spicatum* near *A. saligna* (94%) and *A. acuminata* (81%) was significantly greater than near *A. hemiteles* (45%). At the same age, mean stem diameter of *S. spicatum* growing near *A. saligna* was 53 mm, significantly greater than near *A. acuminata* (33 mm), *A. microbotrya* (20 mm) and *A. hemiteles* (11 mm). Growth was superior at the Dandaragan site, with *S. spicatum* near *A. saligna* having a mean stem diameter of 59 mm and a mean height of 2.3 m.

At host age 4 y, the mean height of *A. microbotrya* (4.3 m) was significantly greater than *A. saligna* (3.3 m), *A. acuminata* (3.2 m) and *A. hemiteles* (1.1 m). Between host ages of 1 y and 4 y, mean survival of *A. saligna* dropped by 27%, significantly more than the other host species (2.5–10%).

Mean potassium and phosphorus concentrations in the foliage of *S. spicatum* were significantly higher near *A. saligna* than near *A. hemiteles*. The mean potassium:calcium ratio was highest near *A. microbotrya* (2.2–3.7) at both sites.

Stem water potentials in *S. spicatum* were significantly lower near *A. microbotrya* (–2.9 MPa) than near *A. hemiteles* (–2.2 MPa) at Dandaragan. There were no significant differences between *S. spicatum* stem water potentials at Narrogin.

Keywords: crop establishment; growth rate; increment; parasitic plants; parasite host relationships; plant nutrition; potassium; phosphorus; water potential; *Santalum spicatum*; *Acacia*; Australia

Introduction

Growing sandalwood (*Santalum spicatum* (R.Br.) A.DC.) trees for their valuable timber has become a real commercial prospect on farmland in south-western Australia. *S. spicatum* is a root hemiparasite (Hewson and George 1984), and therefore needs to be established near suitable host species. Direct seeding *S. spicatum*

near 1–5-y-old *Acacia acuminata* (Benth.) seedlings has been successful on farmland in regions of the midwest and wheatbelt, Western Australia, receiving a mean annual rainfall of 350–600 mm. Mean *S. spicatum* germination rates of over 80% per ‘spot’, and mean survival rates of over 85% after 5–9 y have been achieved (Brand *et al.* 1999; Brand 2002). Between two and four *S. spicatum* seeds are generally planted at each ‘spot’, usually near every second host species, requiring 820–1640 seeds ha⁻¹. This establishment technique is both practical and cost effective, which means that it can be incorporated into revegetation projects. The prospect of a commercial return is an added incentive to plant trees in these relatively dry regions. In Western Australia, over 1000 ha of *S. spicatum* have been successfully established using this technique by a prospectus company called ‘Forest Rewards’ (Peter Grime, *pers. comm.*). The Forest Products Commission and farmers have also successfully established *S. spicatum* by direct seeding near 1–2-y-old *Acacia* seedlings.

Although *S. spicatum* grows slowly (Loneragan 1990), it has a minimum harvestable stem diameter of only 127 mm (measured at 150 mm above ground level) in natural stands. At Northampton, *S. spicatum* planted near *A. acuminata* had stem diameters increasing by 4.5–7 mm y⁻¹, between ages 4 y and 9 y (Brand *et al.* 1999). Near Katanning, mean stem diameters increased by 7–10 mm y⁻¹ between ages 1 y and 5 y (Brand 2002). The predicted time for trees to reach commercial size is about 20 y in the 400–600 mm annual rainfall zone of the wheatbelt (Brand and Jones 1999). *Santalum spicatum* trees grown in plantations are also producing fragrant oils before age 10 y. In a trial at Northampton, core samples from 10-y-old *S. spicatum* trees contained 2.3–2.6% total oil, and the oil contained 16.7–21.1% α - and β -santalol (Brand *et al.* 2001). Santalols are the main compounds that give sandalwood species their distinct fragrance (Adams *et al.* 1975).

It is possible that performance of *S. spicatum* may be further improved with different host species, especially within the genus *Acacia*. Near Katanning, *S. spicatum* growth and survival were significantly higher when planted near *Acacia acuminata* than *Allocasuarina huegeliana* (Miq.) L.Johnson and *Eucalyptus loxophleba* Benth. subsp. *loxophleba* (Brand *et al.* 1999). The *S. spicatum* growing near *A. acuminata* also had significantly higher foliar concentrations of N and K, and a greater K:Ca ratio. In parasitic angiosperms, a high K:Ca ratio indicates that the parasite is successfully drawing on phloem of a suitable host (Tsivion 1978). Increased concentrations of elements in the foliage

of *S. spicatum* may relate to greater nutrient movement from *A. acuminata* to the parasite. The influence of other *Acacia* species on *S. spicatum* growth and nutrient status is of interest.

Parasitic angiosperms typically maintain lower leaf water potentials (Ψ_{leaf}) than their host, which aids in movement of phloem from host to parasite (Fisher 1983). Water potentials indicate the amount of water available to plants (Turner 1981), and low water availability may adversely affect *S. spicatum* performance. *Santalum spicatum* leaf water potentials can vary between host species growing at the same site (Brand *et al.* 2000), which may affect *S. spicatum* growth. Leaf water potentials may influence *S. spicatum* performance near different host species.

This study examined the effect of four different *Acacia* species on *S. spicatum* (i) survival and growth; (ii) foliar nutrient concentration; and (iii) leaf and stem water potentials (Ψ_{leaf} , Ψ_{stem}).

Methods

Two *Acacia* host trials were established on cleared farmland sites at Dandaragan and Narrogin. At Dandaragan (30°30'S, 115°35'E), the soil consisted of a well-drained loamy sand over gravel, while at Narrogin (32°58'S, 117°08'E), the soil was a loamy sand over clay. During winter, water pooled within some sections of the Narrogin site for up to a week after rain. Annual rainfall records during 1998–2001 were obtained from the town of Badgingarra, about 15 km north-west of the Dandaragan trial site, and the town of Narrogin, about 5 km north-east of the Narrogin site.

Between December 1997 and June 1998, *Acacia* seedlings from four potential host species were grown at the Department of Conservation and Land Management Nursery in Narrogin. The four initial host species were *A. acuminata*, *A. microbotrya* (Benth.), *A. saligna* (Labill.) (H.L.Wendl.) and *A. hemiteles* (Benth.). The host seeds were collected from natural populations near Capel (*A. saligna*), Narrogin (*A. microbotrya*) and Bruce Rock (*A. hemiteles*), except for the *A. acuminata* seeds, which were from a plantation of unknown origin, near Esperance.

In March–April 1998, both sites were ripped to a depth of 0.3–0.5 m, in lines spaced 4 m apart. In June–July 1998, the host seedlings (age 6 mo) were planted along the lines at 3 m intervals (833 stems ha⁻¹), in four separate host treatments. Each treatment plot contained 24 initial hosts (i.e. plants near *S. spicatum* that act as hosts after germination) planted along three lines, and 24 long-term hosts (i.e. plants further away from *S. spicatum* that may act as reserve hosts as their root systems expand) planted along three alternate lines. *Acacia acuminata* seedlings were planted as the long-term hosts and these were also from the Esperance plantation. Each of the four treatments was replicated four times, giving a total of 384 initial hosts and 384 long-term hosts planted at each site.

At host age 1 y (April 1999), four *S. spicatum* seeds were sown adjacent to each surviving initial host plant 'spot', with a total of 217 spots sown at Dandaragan and 325 spots sown at Narrogin. *Santalum spicatum* seeds were not planted near the long-term host. The seeds were from a plantation near Narrogin, and were sown 2–3 cm below the surface, 0.5–1.0 m from the base of each host stem. In June 1999, sowing spots were sprayed with glyphosate to control weeds before the *S. spicatum* seedlings emerged.

Survival and growth

Initial host survival was determined at the time of sowing the *S. spicatum* seeds (April 1999). Host survival after sowing the *S. spicatum* seeds was then determined at age 2 y (June 2000), 3 y (June 2001) and 4 y (June 2002). Host height was measured at ages 1 y and 4 y.

The percentage of host spots with at least one *S. spicatum* germinant was recorded in November 1999. Survival and growth were recorded in June 2000 (1 y), June 2001 (2 y), and June 2002 (3 y). The tallest *S. spicatum* seedling at each host spot was measured for height, and stem diameter at 150 mm above the ground. Other *S. spicatum* seedlings at each spot were removed in June 2001.

Foliar analysis

Fresh fully-expanded leaves (*S. spicatum*) and phyllodes (hosts) were collected from each treatment in April 2002. Within each treatment, about 5 g of foliage was collected from 8 *S. spicatum* and 7–8 host plants. These samples were used to determine foliar concentrations of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg). The methods used to obtain these concentrations are described in Brand *et al.* (2000).

Water movement

Pre-dawn (0400–0500 h) leaf water potential (Ψ_{leaf}) of host plants and stem water potential (Ψ_{stem}) of *S. spicatum* within each treatment were measured using a pressure chamber (Scholander *et al.* 1965). *Santalum spicatum* stems were used instead of foliage because the leaves can break in the flexible chamber seal under high pressures (Brand *et al.* 2000). Stem water potential was measured from shoots at points about 5 cm from a young leaf. On 5 February 2002 (Narrogin) and 26 February 2002 (Dandaragan), leaf and stem water potentials were measured from two samples per tree, and six trees per treatment.

Statistical analysis

Germination, survival and growth were compared between treatments and between sites using two-way analysis of variance (ANOVA). Water potential (Ψ_{leaf} and Ψ_{stem}) and element concentration were compared between treatments within each site, using one-way ANOVA. Proportions were angular transformed before analysis and Tukey's test was used to compare means. SYSTAT® was used for all statistical analyses.

Results

Germination and survival

Host species

At age 1 y (April 1999), mean survival of *A. hemiteles* (53.6 ± 7.0%) was significantly lower than survival of the other host species (72.9–76.6%, $P = 0.001$). Mean survival at Narrogin (84.6 ± 3.1%) was significantly greater than at Dandaragan (56.5 ± 4.1%, $P < 0.001$). There was no significant interaction between site and host species ($P = 0.21$).

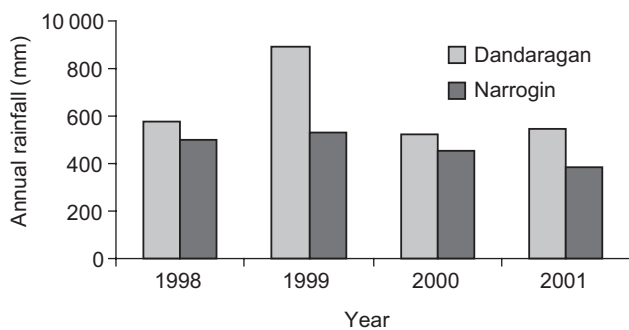


Figure 1. Annual rainfall during 1998–2001, near the Dandaragan site and the Narrogin site

In April 1999, survival of *A. acuminata* planted on alternate lines as the long-term host was similar between treatments (82.3–92.2%, $P = 0.09$) and between sites (84.9–86.5%, $P = 0.67$). There was also no interaction between site and treatment ($P = 0.08$).

Between host ages 1 y (1999) and 4 y (2002), mean survival of *A. saligna* decreased by $27.0 \pm 5.2\%$, significantly more than the other host species (2.5–10.0%, $P = 0.002$). The decrease in host survival was not significantly different between sites ($P = 0.09$), and there was no interaction between site and treatment ($P = 0.33$). *Acacia saligna* mortality was greatest between 2001 and 2002, when survival decreased from 92% to 66% at Dandaragan, and from 99% to 80% at Narrogin.

Mean survival of the long-term host between 1999 and 2002 was not significantly different between sites (88–90%, $P = 0.99$), nor between treatments (76–94%, $P = 0.31$). There was also no interaction between site and treatment ($P = 0.94$).

Annual rainfall between 1998 and 2001 was 529–897 mm near Dandaragan and 383–532 mm near Narrogin (Fig. 1). Mean annual rainfall during this period was 639 mm near Dandaragan and 468 mm near Narrogin.

Sandalwood

The mean germination rates of *S. spicatum* per spot at Dandaragan ($90.6 \pm 2.7\%$) and Narrogin ($80.7 \pm 3.7\%$) were not significantly different ($P = 0.13$). Mean *S. spicatum* germination was similar between host treatments (83.6–88.5%, $P = 0.94$) and there was no significant interaction between site and treatment ($P = 0.06$).

At age 3 y, *S. spicatum* seedling survival was significantly greater near *A. saligna* ($94.3 \pm 4.2\%$) and *A. acuminata* ($80.9 \pm 5.9\%$) than *A. hemiteles* ($45.3 \pm 7.2\%$, $P < 0.001$). Mean survival of *S. spicatum* near *A. microbotrya* was $63.7 \pm 8.2\%$. Mean survival of *S. spicatum* was not significantly different between sites (67.3–74.7%, $P = 0.33$), and there was no interaction between site and host treatment ($P = 0.94$).

Between sites, mean survival of 3-y-old *S. spicatum* (Fig. 2) near *A. saligna* was greater at Dandaragan ($96.9 \pm 3.1\%$) than at Narrogin ($91.7 \pm 8.3\%$). Mean survival of *S. spicatum* near *A. acuminata* was also greater at Dandaragan ($84.7 \pm 6.3\%$) than at Narrogin ($77.0 \pm 10.5\%$). In the first year, 38.6–42.8% of *S. spicatum* died near *A. hemiteles* at both sites.

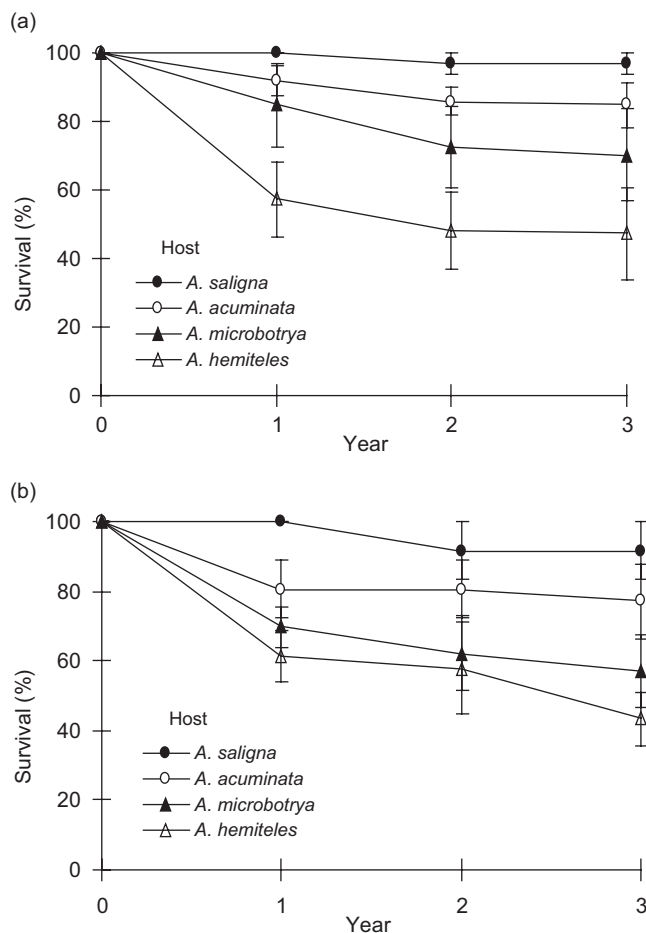


Figure 2. Mean *Santalum spicatum* survival (\pm std errors) next to four different *Acacia* species at (a) Dandaragan and (b) Narrogin

Growth

Host species

When the parasite was introduced in May 1999, the mean height of *A. saligna* (1.7 ± 0.03 m) was significantly greater than the heights of other hosts ($F_{3,534} = 239$, $P < 0.001$). *Acacia microbotrya* (1.4 ± 0.03 m) and *A. acuminata* (1.4 ± 0.03 m) were also significantly taller than *A. hemiteles* (0.4 ± 0.04 m). Host trees at Dandaragan (1.3 ± 0.02 m) were significantly taller than at Narrogin (1.2 ± 0.02 m; $F_{1,534} = 18.2$, $P < 0.001$). There was also a significant interaction between site and treatment ($F_{3,534} = 4.4$, $P = 0.005$), but this was minor compared to the main effects of host treatment and site.

At host age 4 y (July 2002), the mean height of *A. microbotrya* (4.3 ± 0.1 m) was significantly greater than the heights of other treatments ($F_{3,481} = 443$, $P < 0.001$). *Acacia saligna* (3.3 ± 0.1 m) and *A. acuminata* (3.2 ± 0.1 m) were both significantly taller than *A. hemiteles* (1.1 ± 0.1 m). The host trees were again significantly taller at Dandaragan (3.2 ± 0.05 m) than at Narrogin (2.7 ± 0.04 m; $F_{1,481} = 60.4$, $P < 0.001$). A significant interaction occurred between site and treatment ($F_{3,534} = 10.5$, $P < 0.001$), but this was again minor compared to the main effects.

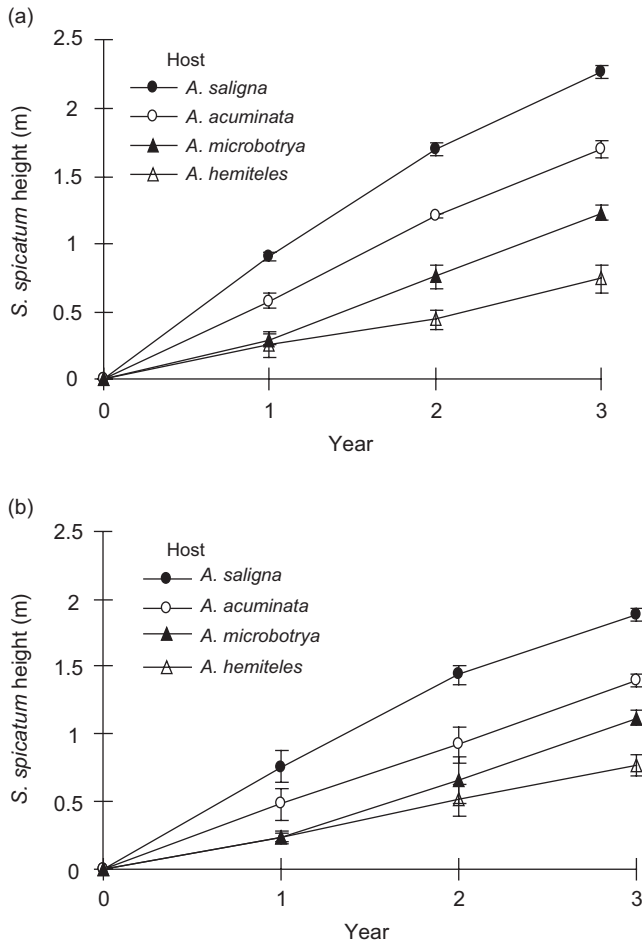


Figure 3. Mean *Santalum spicatum* height (\pm std errors) next to four different *Acacia* species at (a) Dandaragan and (b) Narrogin

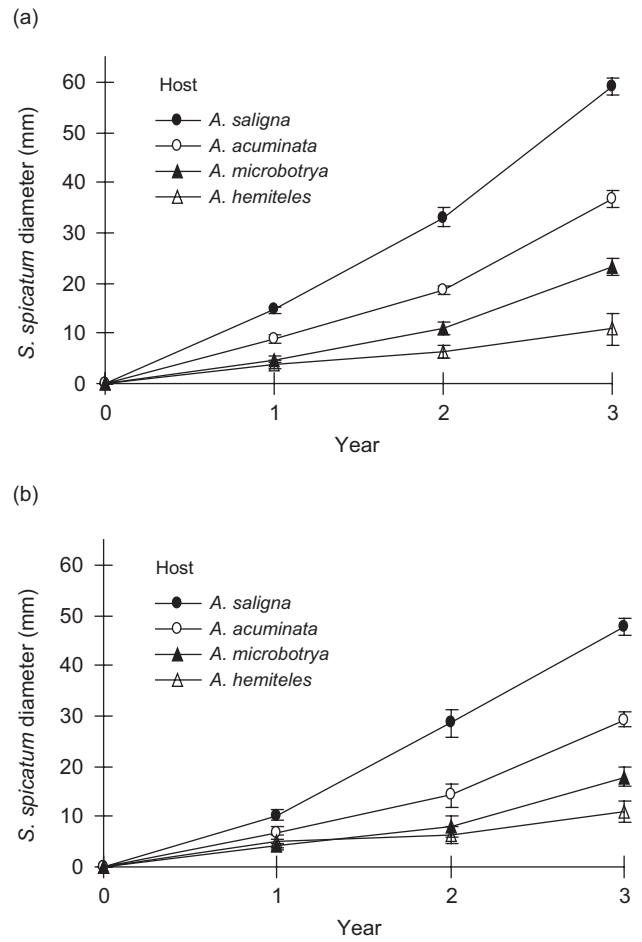


Figure 4. Mean *Santalum spicatum* stem diameter (\pm std errors) next to four different *Acacia* species at (a) Dandaragan and (b) Narrogin

Sandalwood

At age 3 y, *S. spicatum* seedling height was significantly greater near *A. saligna* (2.1 ± 0.1 m) than near *A. acuminata* (1.6 ± 0.1 m), *A. microbotrya* (1.2 ± 0.1 m) and *A. hemiteles* (0.8 ± 0.1 m; $F_{3,347} = 148, P < 0.001$). The mean height of *S. spicatum* at Dandaragan (1.5 ± 0.04 m) was significantly greater than at Narrogin (1.3 ± 0.03 m, $F_{3,347} = 148, P < 0.001$). There was an interaction between site and host treatment ($F_{3,347} = 3.8, P = 0.011$), but this was minor compared to the main effects of host treatment and site.

Santalum spicatum stem diameter was significantly greater near *A. saligna* (53.4 ± 1.0 mm, $P < 0.001$) than near *A. acuminata* (33.1 ± 1.2 mm), *A. microbotrya* (20.5 ± 1.3 mm) and *A. hemiteles* (10.8 ± 2.0 mm). The mean stem diameter of *S. spicatum* at Dandaragan (32.5 ± 1.1 mm) was significantly greater than at Narrogin (26.4 ± 0.9 mm, $P < 0.001$). Stem diameter in *S. spicatum* did not have a significant interaction between site and host treatment ($P = 0.051$).

Within sites, the largest *S. spicatum* were near *A. saligna* at Dandaragan. At age 3 y, these *S. spicatum* had a mean height of 2.3 ± 0.1 m (Fig. 3), and a mean stem diameter of 59.1 ± 1.1 mm (Fig. 4). Between 1999 and 2002, these *S. spicatum* were increasing in height by $0.6\text{--}0.9$ m y^{-1} and their stem diameters were increasing by $15\text{--}26$ mm y^{-1} . Mean stem diameter of *S. spicatum* near

A. acuminata was also greater at Dandaragan (36.8 ± 1.8 mm), with the diameters increasing by $9\text{--}18$ mm y^{-1} .

Foliar analysis

Concentrations of elements in *S. spicatum* foliage varied significantly between host treatments, but the pattern of variation was not always the same between sites (Table 1). However, the mean concentration of K was significantly greater when *S. spicatum* was near *A. saligna* ($17.3\text{--}23.3$ mg g^{-1}) than when it was near *A. hemiteles* ($9.5\text{--}9.6$ mg g^{-1}), at both sites. *S. spicatum* growing near *A. microbotrya* had the highest K:Ca ratios ($2.2\text{--}3.7$). The concentration of P was significantly greater in *S. spicatum* near *A. saligna* (2.3 mg g^{-1}) than *A. hemiteles* ($0.8\text{--}1.0$ mg g^{-1}), at both sites.

Water movement

In February 2002, the pre-dawn leaf and stem water potentials of *S. spicatum* were the same as, or significantly lower than, those of their paired hosts, at both sites (Table 2). At Dandaragan, pre-dawn stem water potentials of *S. spicatum* were significantly lower when it was near *A. microbotrya* (-2.9 ± 0.2 MPa) and *A. acuminata* (-2.8 ± 0.1 MPa) than when it was near *A. saligna* (-2.1 ± 0.1 MPa). However, at Narrogin, stem water potentials were

Table 1. Mean concentrations (\pm std errors) of elements in the foliage of *Santalum spicatum* growing with four *Acacia* species ($n = 7-8$), at Dandaragan and Narrogin

Species	Element					
	N (mg g ⁻¹)	P (mg g ⁻¹)	K (mg g ⁻¹)	Ca (mg g ⁻¹)	Mg (mg g ⁻¹)	K:Ca ratio
(a) Dandaragan						
<i>A. saligna</i>	24.7 \pm 1.4 a	2.3 \pm 0.2 a	23.3 \pm 2.0 a	13.8 \pm 0.8 ab	3.0 \pm 0.3 ab	1.7 \pm 0.1
<i>A. acuminata</i>	25.2 \pm 1.6 a	1.6 \pm 0.2 b	14.1 \pm 2.2 b	12.4 \pm 1.2 ab	1.5 \pm 0.2 b	1.3 \pm 0.2
<i>A. microbotrya</i>	21.0 \pm 3.0 ab	1.2 \pm 0.2 bc	15.2 \pm 2.1 ab	9.7 \pm 1.8 b	2.4 \pm 0.6 b	2.2 \pm 0.6
<i>A. hemiteles</i>	15.3 \pm 2.9 b	0.8 \pm 0.1 c	9.6 \pm 1.9 b	17.3 \pm 0.2 a	5.4 \pm 1.2 a	0.7 \pm 0.2
<i>P</i> -value	0.010	< 0.001	0.001	0.014	0.006	0.056
(b) Narrogin						
<i>A. saligna</i>	17.3 \pm 1.0 b	2.3 \pm 0.3 a	17.3 \pm 0.6 a	16.0 \pm 1.7 a	3.6 \pm 0.4 a	1.2 \pm 0.1 b
<i>A. acuminata</i>	16.0 \pm 1.2 b	1.8 \pm 0.2 ab	15.0 \pm 1.6 ab	14.5 \pm 2.4 ab	2.7 \pm 0.8 a	1.1 \pm 0.2 b
<i>A. microbotrya</i>	26.0 \pm 2.2 a	2.7 \pm 0.3 a	15.7 \pm 2.0 a	5.0 \pm 0.6 c	0.8 \pm 0.1 b	3.7 \pm 0.8 a
<i>A. hemiteles</i>	18.6 \pm 1.3 b	1.0 \pm 0.1 b	9.5 \pm 1.5 b	8.9 \pm 1.7 bc	3.5 \pm 0.8 a	1.1 \pm 0.1 b
<i>P</i> -value	< 0.001	< 0.001	0.007	< 0.001	0.001	< 0.001

Values with the same letter are not significantly different, using Tukey's test ($P > 0.05$).

similar between *S. spicatum* treatments (-2.0 to -2.4 MPa). Within host species, the leaf water potentials were generally similar between treatments, but were highest near *A. hemiteles* (-1.0 to -1.2 MPa).

Discussion

Santalum spicatum survival was significantly greater near *A. saligna* (94.3%) and *A. acuminata* (80.9%) than near *A. hemiteles* (45.3%), at age 3 y. *S. spicatum* seedling growth was also significantly better near *A. saligna* than near the other host species. At the same age, mean stem diameter of *S. spicatum* growing near *A. saligna* was 53.4 mm, which is twice that reported for *S. spicatum* of similar age growing near *A. acuminata* (Brand *et al.* 2000). At Dandaragan, the mean stem diameter of *S. spicatum* near *A. saligna* was 59.1 mm, with the stems increasing 15–26 mm y⁻¹. This is relatively fast growth for *S. spicatum*, which typically increases only 1–2 mm y⁻¹ in natural conditions near Kalgoorlie (Loneragan 1990), and 4.5–9 mm y⁻¹ in wheatbelt plantations (Brand *et al.* 1999, 2000).

Acacia saligna appears to be an excellent initial host species for *S. spicatum*. The *A. saligna* provenance used in this trial was relatively fast growing, with a mean height of 1.7 m at age 1 y, and 3.3 m at age 4 y. A benefit of fast initial host growth is that *S. spicatum* can be established at host age 1 y instead of age 2 y. When the seeds were sown in 1999, more host roots were observed beneath the *A. saligna* than beneath any other host species. This may have enabled more successful haustorial attachments at an early age. Although there has been fast initial growth of *S. spicatum* near *A. saligna*, this host species may not live long enough to support *S. spicatum* through to harvestable size, at perhaps age 15–20 y. Between host ages 1 and 4 y, mean survival of *A. saligna* dropped by 27%, a significantly greater decline than seen in the other hosts. This species seems best as an initial host, planted in conjunction with a long-term host such as *A. acuminata*. The Indian sandalwood (*Santalum album* Linn.) is typically established using a pot host, an intermediate host and a long-term host

(Radomiljac 1998) to maximise growth at each stage. Similarly, *S. spicatum* growth could be improved by growing fast near *A. saligna* before attaching to *A. acuminata*. Trials are needed to assess the effect of different ratios of *A. saligna* and *A. acuminata* on *S. spicatum* performance initially and through to harvest.

Mean stem diameter of *S. spicatum* near *A. acuminata* was 33.1 mm at age 3 y, which is still relatively good growth. At the same age, mean stem diameter of *S. spicatum* near *A. microbotrya* was only 20.5 mm. The *A. microbotrya* provenance used in this trial was relatively fast growing, with a mean height of 1.4 m at age 1 y, and 4.3 m at age 4 y. However, unlike *A. saligna*, relatively fast host growth did not correspond to fast growth in *S. spicatum*. This indicates that fast-growing *Acacia* species do not always improve *S. spicatum* performance. Survival and growth of *S. spicatum* were lowest near *A. hemiteles*, and this species does not appear to be a suitable host in the wheatbelt.

Mean growth of *S. spicatum* was significantly greater at Dandaragan than Narrogin. During 1998–2001, the mean annual rainfall at Dandaragan was 639 mm compared to 468 mm at Narrogin. The relatively high rainfall at Dandaragan may have improved *S. spicatum* performance. Differences in soil type may have also influenced growth: the Dandaragan site has a loamy sand over gravel, while Narrogin has a loamy sand over clay.

The mean concentrations of K and P in foliage were significantly greater in *S. spicatum* near *A. saligna* than near *A. hemiteles*. Fast growth in *S. spicatum* near *A. saligna* may be related to this species providing higher concentrations of K to the parasite. Brand *et al.* (2000) also found that the foliar concentration of K and seedling growth were significantly greater in *S. spicatum* near *A. acuminata* than near *A. huegeliana*. However, the K:Ca ratio in *S. spicatum* was highest near *A. microbotrya*. High K:Ca ratios have also been related to fast initial growth in both *S. album* (Radomiljac *et al.* 1998) and *S. spicatum* (Brand *et al.* 2000), but in this study *S. spicatum* growth was significantly less near *A. microbotrya* than near *A. saligna* and *A. acuminata*.

Table 2. Pre-dawn leaf and stem water potentials (MPa \pm std errors) of *Santalum spicatum* and host trees. Measurements were made on 5 February 2002 (Narrogin) and 28 February 2002 (Dandaragan), ($n = 6$ to 8).

Host/parasite	Location	
	Dandaragan	Narrogin
<i>A. microbotrya</i> / <i>S. spicatum</i>	-2.3 \pm 0.2 abc	-1.4 \pm 0.1 bc
<i>A. acuminata</i> / <i>S. spicatum</i>	-2.2 \pm 0.1 bc	-2.2 \pm 0.2 a
<i>A. saligna</i> / <i>S. spicatum</i>	-2.8 \pm 0.1 ab	-2.3 \pm 0.2 a
<i>A. saligna</i> / <i>S. spicatum</i>	-1.6 \pm 0.2 cd	-1.9 \pm 0.1 ab
<i>A. hemiteles</i> / <i>S. spicatum</i>	-2.1 \pm 0.1 c	-2.0 \pm 0.2 ab
<i>A. hemiteles</i> / <i>S. spicatum</i>	-1.0 \pm 0.1 d	-1.2 \pm 0.1 c
<i>S. spicatum</i>	-2.2 \pm 0.2 abc	-2.4 \pm 0.2 a
P-value	< 0.001	< 0.001

Values with the same letter are not significantly different, using Tukey's test ($P > 0.05$)

Within *S. spicatum* treatments, pre-dawn stem water potentials were significantly lower near *A. microbotrya* (-2.9 MPa) than near *A. saligna* (-2.1 MPa) at Dandaragan, but were similar at Narrogin (-2.0 to -2.4 MPa). These pre-dawn stem water potentials for *S. spicatum* are relatively high for summer. Brand *et al.* (2000) recorded mean pre-dawn stem water potentials of -4.0 MPa in 3-y-old *S. spicatum* near Katanning. It appears that water availability was relatively good for all *S. spicatum* treatments at both sites and there were no obvious relationships between stem water potential and *S. spicatum* growth.

Conclusion

Initial *S. spicatum* growth was far superior near *A. saligna*, with mean stem diameters increasing by 15–26 mm y^{-1} at Dandaragan. This host species is vigorous and has the advantage of being suitable for a parasite at host age 1 y instead of 2 y. It has the disadvantage, however, of being short-lived, with 27% of the trees dead at age 4 y. *Santalum spicatum* requires host trees for about 15–20 y if it is to reach commercial size. Planting *A. saligna* as an initial host, together with *A. acuminata* as a long-term host, may be a suitable combination to improve *S. spicatum* growth rate over 20 y. Further research should examine different combinations of *A. acuminata* and *A. saligna* to identify the best planting arrangement. Although *S. spicatum* performed significantly better near *A. saligna*, this did not appear to be related to mean foliar element concentrations or stem water potentials. The results of this study, however, conform with the finding of Brand *et al.* (2000), that K appears to be an important element which *S. spicatum* gains from suitable host species.

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