

## Why is *Santalum spicatum* common near granite rocks?

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### Abstract

Sandford Rocks Nature Reserve is dominated by a large granite outcrop. This reserve is notably well-endowed with trees of the root parasite sandalwood (*Santalum spicatum*). These are comparatively common in and among granite exposures. Trees attain 4 m in height and 20 cm basal diameter on favourable sites but are small gnarled shrubs in rock fissures. Fruiting ability differs considerably between trees. Despite apparently high densities of rabbits, continuous regeneration appears to have occurred, but only in the vicinity of parent trees. The reserve contains a number of distinct vegetation associations that are soil determined. Although sandalwood is common near exposed granite it is rarely found in association with *Eucalyptus* stands. It is suggested that the water-shedding properties of the granite exposures are less important to sustaining sandalwood than the presence of preferentially parasitised host species.

### Introduction

Most investigations of parasitism have been concerned with relatively short lived species (Matthies 1995) and although parasitic plants may have major impacts on structure and dynamics of natural vegetation (Pennings & Callaway 1996), little is known of their regeneration. Confirmation that particular host species can enable long-lived parasitic plants to perform better under field conditions is time consuming but a necessary prerequisite if such species are to be cultivated (Fox *et al.* 1996). Perennial woody semi-parasites tend to have larger seed (Musselman & Mann 1978) than invasive shrubs (Grice 1996) and longer-lived perennials are likely to have temporally distinct growth phases.

In much of the eastern wheatbelt of Western Australia the obligate semi-parasitic small tree sandalwood (*Santalum spicatum* [R Br] A DC) is now uncommon. This species was the most valuable natural product to settlers and was severely exploited from about the turn of the century after the railway reached Southern Cross in 1894 (Loneragan 1990) and is now absent from some areas (Lange 1960). It remains an important and valuable resource in more arid regions of the State, accounting for some \$7 million in royalties paid to the Department of Conservation and Land Management in 1993–94. That represents some 22 % of all royalty revenue, only marginally less than that from woodchips (Anon 1994). A management plan for sandalwood was prepared in 1991 (Kealley 1991). Little is known of the impact of *S. spicatum* on natural plant communities.

### Study Area and Methods

Sandford Rock Nature Reserve (SRNR) lies 9 km north east of the small town of Westonia (31° 15' S, 118° 45' E). Curtin University has undertaken research into the vegetation of the reserve since 1991. The family

Santalaceae is represented by three small tree species: *Exocarpos aphyllus* R Br (leafless ballart), *Santalum acuminatum* (R Br) A DC (quandong) and *Santalum spicatum* (sandalwood). The latter is known to parasitise a number of potential hosts, usually including acacias (e.g. *A. acuminata* Benth, *A. aneura* F Muell ex Benth, and *A. tetragonophylla* F Muell), *Allocasuarina*, *Melaleuca* and some herbaceous species. Eucalypts are not considered to be good hosts (Barrett & Fox 1995). Eight of 17 species recorded as hosts to *Santalum spicatum* by Loneragan (1990) occur at SRNR. The Reserve contains at least 14 species of *Eucalyptus*, 4 species of *Allocasuarina* and 9 species of *Melaleuca* (Fox *et al.* 1993). Up to 25 species of *Acacia* occur, often in well-defined habitats. These numbers compare with those of Hopper *et al.* (1997) of 83 *Acacia* and 25 *Melaleuca* for granite outcrops generally.

The climatic regime is described by Beard (1981) as extra dry mediterranean. The mean annual rainfall is around 330 mm and some summer rain is usually experienced (Fig 1). Water shed from the massive complex of granite occupying the centre of the reserve

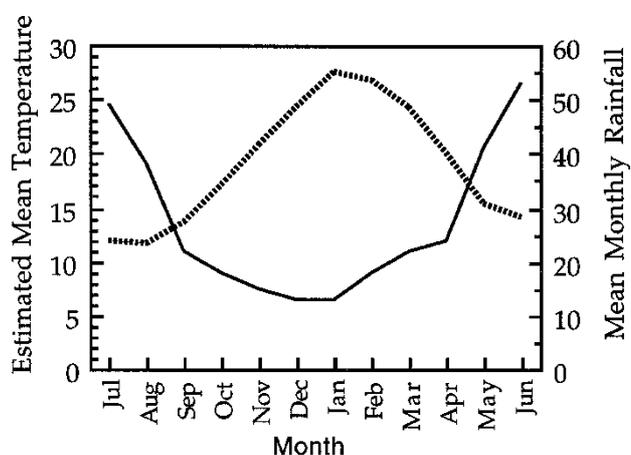


Figure 1. Estimated mean temperature (°C; broken line) and mean monthly rainfall (mm; solid line) for the study area near Westonia.

fills rock pools in winter, drives an ephemeral stream and probably contributes to underground aquifers supplying eucalypt stands of the area through the drier months.

SRNR occupies a land area of ~800 ha (Fig 2). On and around the granite exposures, soil pockets of variable depth occur, with heath or shrubland while the surrounding flats carry shrublands or woodlands. Within the reserve a mosaic of soil types is reflected in the dominating suites of plant species. The vegetation is described by Muir (1979) as jam woodland on moderately well-drained pinkish grey, gritty loam; gimlet woodland on poorly drained red, sandy clay; wandoo (with scattered salmon gum) and York gum woodland mainly on poorly drained pinkish grey, sandy clay loam; mallee with *Acacia acuminata* and *A. stereophylla* Meissner in Lehm, on light reddish brown, loams and *Acacia hemiteles* Benth on areas of heavier soil, poorly drained, of pinkish grey, sandy clay. Tamma shrubland is present (*Allocasuarina campestris* (Diels) L Johnson or *A. acutivalvis* (F Muell) L Johnson) with *Acacia stereophylla* locally co-dominant. Tamma soils are well-drained brownish yellow, fine sandy loams, with 40– 60% laterite in some areas. Granitic soils at SRNR are similar to those at Durokoppin Nature Reserve (31 °

23' S, 117 ° 46' E) described by McArthur (1991). The Southern Cross mallee (*Eucalyptus crucis* Maiden) occurs in thickets of myrtaceous scrub in relatively deep and well watered soil around the edges of the exposed rock. Fire has not occurred in SRNR since at least 1927 (Fox *et al.* 1993).

Reconnaissance indicated that sandalwood trees are frequent in 4 general localities (Fig 2). The first, PA, is in the vicinity of a picnic site in the south west. Here, sandalwood occurs in low mixed woodland, among and adjacent to *Acacia* species and *Allocasuarina huegeliana* (Miq) Johnson, near an ephemeral stream. The second, to the north and east of PA, covers several loosely defined areas (with the prefix R). These areas lie adjacent to large granite exposures and are mainly associated with narrow bands of mixed woodland (R) or *Allocasuarina huegeliana* (RE). One set is to the south of a major overhang (RO); another (RS), is associated with thickets of *Leptospermum erubescens* Schauer in Lehm. The third and fourth localities are further north and lie between major rock exposures; in one case (CK 3) adjacent to dense stands of eucalypt woodland, and in the second, among patches of *Allocasuarina huegeliana* and adjacent to another rock exposure (CK 3B).

At these localities, sandalwood trees have been

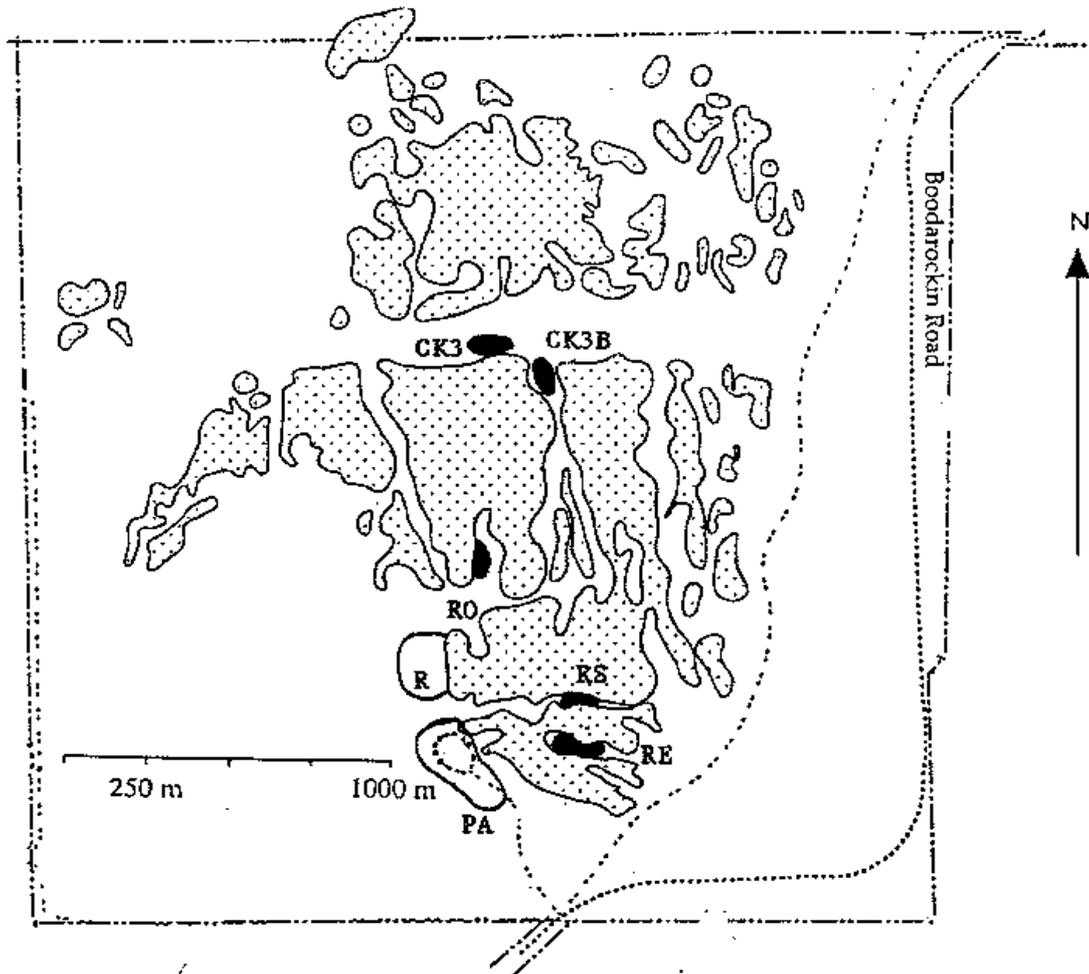


Figure 2. Plan of the Sandford Rocks Nature Reserve, showing sandalwood sample areas.

mapped and measured for height, crown widths and stem diameters at 5, 15 and 130 cm above ground level. Observations on flowering have been made and fallen nuts from the previous years' crops have been counted in March. Soil depth in the vicinity of sandalwood trees has been obtained from a mean of 3 probes. Adjacent perennial species have been recorded. Sandalwood seedlings are counted when present.

## Results

### Stocking

Most measured trees are 200–400 cm tall (70%), with only 10 of 161 enumerated in 1996 of >400 cm in height (Table 1). Mean heights by localities at March 1996 are: PA- 258 cm  $\pm$  se 13 (n= 39); CK3- 244 cm  $\pm$  se 10 (n= 54); CK3B- 301 cm  $\pm$  se 17 (n= 34); and R- 265 cm  $\pm$  se 16 (n= 34). Distribution within 50 cm height classes is illustrated (Fig 3). The whole population has a normal height class distribution but the four localities differ. R trees depart most from normal distribution with two peaks. The

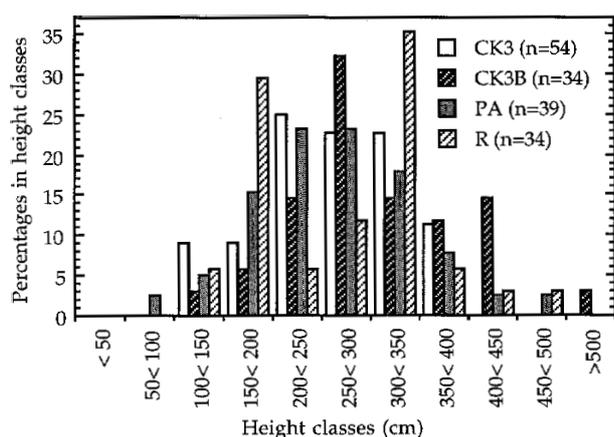


Figure 3. Plants closest to the rocks are less normally distributed in height class than those further away.

small spread of heights at CK3 probably reflects inter-plant competition. The high proportion of taller trees at CK3B may indicate best growing conditions.

Mean stocking of sandalwood on 5.83 ha sampled (excluding area R where trees are scattered individuals across a large area) is 26.1 trees ha<sup>-1</sup>. The density of sandalwood trees is very variable. For the 2.5 ha of woodland sampled at PA, where no tree is near any exposed granite, and all lie west of the stream, the mean number of trees is 15.6 ha<sup>-1</sup> (Table 1). On the rocky sites, where the area taken is that occupied by trees and shrubs, stocking varies from 5.5 ha<sup>-1</sup> on 2 ha constituting the east patch of *Allocasuarina huegeliana* (RE), through 18 ha<sup>-1</sup> on 0.33 ha of mainly *Leptospermum erubescens* thicket (RS), to 40 ha<sup>-1</sup> on the 0.2 ha of mixed vegetation at RO. Stocking is highest at the localities adjacent to granite: 180 ha<sup>-1</sup> on 0.3 ha at CK3 and 68 ha<sup>-1</sup> on 0.5 ha at CK3B.

Sandalwood trees tend to be grouped and at each of PA, CK3 and CK3B clumps of 4–30 trees are treated separately as subsets (Table 1). These clumps occupy areas of 40 to 100 m<sup>2</sup> and have local densities of 400–3 000 trees ha<sup>-1</sup>. Seedlings (sandalwoods generally <150 cm tall) also tend to be clumped and are not currently found away from parent trees.

### Hosts

Some 48 different perennial plant species from 23 families occur in the vicinity of the measured sandalwood trees taken as 110 individuals or clumps (Table 2). Those listed include most of the important perennials found in vegetation adjacent to sandalwood at the four localities examined. The species *Acacia acuminata*, *Dianella revoluta*, *Dodonaea inaequifolia* and *Allocasuarina huegeliana* appear most frequently. The localities differ, with more species recorded at R sites (31 species; mean species per sandalwood 3.5) and least at PA and CK3 (14 species; mean species per sandalwood 3 and 2.5 respectively). Locality CK3B, with 24 species has most co-occurrences per sandalwood (8).

Despite the large number of *Acacia* species present in SRNR, only *A. acuminata* appears to be important as a potential host. It is the most frequent species at 3 of the 4

Table 1

Stocking data for designated sample areas at Sandford Rock Nature Reserve.

Locality <sup>1</sup>	Sample area <sup>2</sup> (m <sup>2</sup> )	Seedlings <sup>3</sup>	Number of sandalwoods by height classes (cm)				Number ha <sup>-1</sup>	
			< 200	200-300	300-400	>400	Trees only	All plants
PA	25 000	63	9	18	10	2	15.6	40.8
Sub-set a	50	0	2	5	1	1	1 800	1 800
Sub-set b	40	36	0	5	0	0	1 250	10 250
R	diffuse <sup>4</sup>	56	3	3	3	0	nc <sup>4</sup>	nc <sup>4</sup>
RE	20 000	0	4	3	4	0	5.5	5.5
RS	3 333	0	4	0	2	0	18	18
RO	2 000	9	1	0	5	2	40	85
CK3	3 000	41	15	24	15	0	180	316
Sub-set a	100	30	7	15	8	0	3 000	6 000
CK3B	5 000	119	3	16	9	6	68	306
Sub-set a	100	29	0	1	1	2	400	3 300

<sup>1</sup> See Figure 2 for localities. <sup>2</sup> The sub-sets represent small areas of concentrated *Santalum spicatum* plants. <sup>3</sup> Seedlings generally < 150 cm tall. <sup>4</sup> nc= not calculated

Table 2

Frequency of occurrence of 110 trees or clumps of *Santalum spicatum* with other perennial species at 4 localities within Sandford Rocks Nature Reserve; number (#) and percentage (%).

Possible host species (ranked alphabetically in order of frequency)	Family	Life form	Locality [as in Table 1]								All as % (n= 110)
			R (n= 34)		CK 3 (n=17)		CK 3B (n=32)		PA (n= 27)		
			#	%	#	%	#	%	#	%	
<i>Acacia acuminata</i> Benth	Mimosaceae	Tree	10	29	15	88	25	78	18	67	62
<i>Dianella revoluta</i> R Br	Phormiaceae	Herbaceous	7	21	2	12	28	88	1	4	35
<i>Dodonaea inaequifolia</i> Turcz	Sapindaceae	Medium shrub	11	32	1	6	12	38	14	52	35
<i>Allocasuarina huegeliana</i> (Miq) L Johnson	Casuarinaceae	Tree	9	26	2	12	25	78	-	-	33
<i>Dodonaea viscosa</i> Jacq	Sapindaceae	Medium shrub	14	41	-	-	17	53	-	-	28
<i>Comesperma volubile</i> Labill	Polygalaceae	Twiner	2	6	-	-	19	59	-	-	19
<i>Chamaexeros fimbriata</i> (F Muell) Benth	Dasypogonaceae	Herbaceous	8	24	-	-	12	38	-	-	18
<i>Eucalyptus loxophleba</i> Benth	Myrtaceae	Mallee	1	3	1	6	3	9	15	56	18
<i>Hibbertia glomerata</i> (Benth) F Muell	Dilleniaceae	Low shrub	-	-	-	-	20	63	-	-	18
<i>Lepidosperma gracile</i> R Br	Cyperaceae	Sedge	4	12	-	-	13	41	1	4	16
<i>Stipa elegantissima</i> Labill	Poaceae	Grass	-	-	-	-	18	56	-	-	16
<i>Allocasuarina campestris</i> (Diels) L Johnson	Casuarinaceae	Medium shrub	2	6	2	12	13	41	-	-	15
<i>Alyxia buxifolia</i> R Br	Apocynaceae	Tall shrub	1	3	-	-	6	19	9	33	15
<i>Calothamnus asper</i> Turcz	Myrtaceae	Medium shrub	3	9	5	29	5	16	-	-	12
<i>Hakea recurva</i> Meissner in DC	Proteaceae	Medium shrub	3	9	-	-	-	-	8	30	10
<i>Leptospermum erubescens</i> Schauer in Lehm	Myrtaceae	Medium shrub	7	20	4	24	-	-	-	-	10
<i>Melaleuca hamulosa</i> Turcz	Myrtaceae	Tall shrub	-	-	3	18	6	19	-	-	8
<i>Melaleuca radula</i> Lindley	Myrtaceae	Medium shrub	-	-	2	12	7	22	-	-	8
<i>Lepidosperma drummondii</i> Benth	Cyperaceae	Sedge	8	23	-	-	-	-	-	-	7
<i>Solanum nummularium</i> S Moore	Solanaceae	Low shrub	2	6	-	-	6	19	-	-	7
<i>Stypandra imbricata</i> R Br	Phormiaceae	Herbaceous	1	3	-	-	6	19	-	-	6
<i>Eucalyptus capillosa</i> Brooker & Hopper	Myrtaceae	Tree	-	-	1	6	-	-	4	15	5
<i>Grevillea paniculata</i> Meissner in Lehm	Proteaceae	Medium shrub	5	15	-	-	-	-	-	-	5
<i>Hibbertia exasperata</i> (Steudel) Briq	Dilleniaceae	Low shrub	6	18	-	-	-	-	-	-	5
<i>Keraudrenia integrifolia</i> Steudel in Lehm	Sterculiaceae	Low shrub	-	-	-	-	5	16	-	-	5
<i>Rhagodia drummondii</i> Moq in DC	Chenopodiaceae	Low shrub	-	-	-	-	5	16	-	-	5
<i>Acacia hemiteles</i> Benth	Mimosaceae	Medium shrub	-	-	-	-	-	-	4	15	4
<i>Solanum lasiophyllum</i> Dunal ex Poirlet	Solanaceae	Low shrub	-	-	-	-	3	9	1	4	4
<i>Spartochloa scirpoidea</i> (Steudel) C E Hubb	Poaceae	Grass	4	12	-	-	-	-	-	-	4
<i>Acacia erinacea</i> Benth	Mimosaceae	Low shrub	1	3	-	-	-	-	2	7	3
<i>Allocasuarina acutivalvis</i> (F Muell) L Johnson	Casuarinaceae	Medium shrub	-	-	-	-	3	9	-	-	3
<i>Cassia nemophila</i> Cunn ex Vogel	Caesalpinaceae	Medium shrub	2	6	1	6	-	-	-	-	3
<i>Daviesia nematophylla</i> F Muell ex Benth	Papilionaceae	Medium shrub	-	-	-	-	3	9	-	-	3
<i>Scaevola spinescens</i> R Br	Goodeniaceae	Low shrub	-	-	-	-	-	-	3	11	3
<i>Solanum orbiculatum</i> Dunal	Solanaceae	Low shrub	-	-	-	-	3	9	-	-	3
<i>Acacia colletioides</i> Benth	Mimosaceae	Tall shrub	-	-	-	-	-	-	2	7	2
<i>Acacia saligna</i> (Labill) Wendl	Mimosaceae	Tall shrub	2	6	-	-	-	-	-	-	2
<i>Astroloma serratifolium</i> (DC) Druce	Epacridaceae	Low shrub	2	6	-	-	-	-	-	-	2
<i>Melaleuca macronychia</i> Turcz	Myrtaceae	Medium shrub	1	3	1	6	-	-	-	-	2
<i>Olearia revoluta</i> F Muell ex Benth	Asteraceae	Low shrub	-	-	2	12	-	-	-	-	2
<i>Baeckea behrii</i> (Schldl) F Muell	Myrtaceae	Tall shrub	1	3	-	-	-	-	-	-	<1
<i>Billardiera erubescens</i> (Putterl) E M Bennett	Pittosporaceae	Twiner	1	3	-	-	-	-	-	-	<1
<i>Eremophila scoparia</i> (R Br) F Muell	Myoporaceae	Low shrub	1	3	-	-	-	-	-	-	<1
<i>Eucalyptus crucis</i> Maiden	Myrtaceae	Tree	1	3	-	-	-	-	-	-	<1
<i>Melaleuca uncinata</i> R Br in W T Aiton	Myrtaceae	Tall shrub	-	-	-	-	1	3	-	-	<1
<i>Persoonia striata</i> R Br	Proteaceae	Medium shrub	1	3	-	-	-	-	-	-	<1
<i>Pittosporum phylliraeoides</i> DC	Pittosporaceae	Tree	-	-	-	-	-	-	1	4	<1
<i>Pityrodia teckiana</i> (F Muell) E Pritzel	Chloanthaceae	Low shrub	1	3	-	-	-	-	-	-	<1

Botanical nomenclature after Green (1985). Life forms: tree – a single stem; mallee – multi-stemmed *Eucalyptus*; tall shrub – mature individuals > 2m in height; medium shrub – mature individuals > 1 m tall, but not > 3 m; low shrub – generally < 1 m tall.

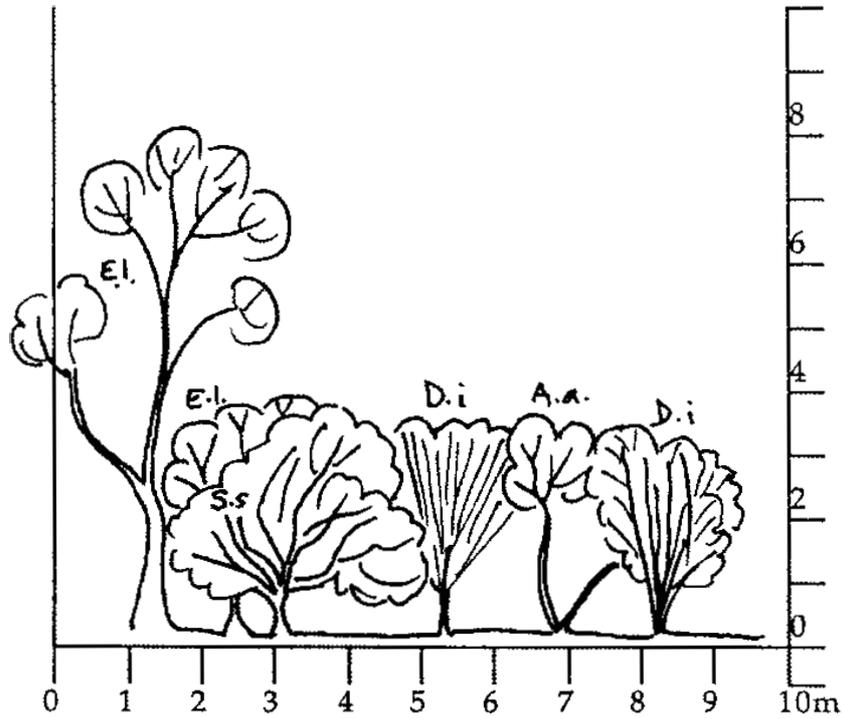


Figure 4. Profile (tree 10; ht 377 cm, stand of *Santalum spicatum* (S.s.) with *Eucalyptus loxophleba* (E.l.) with *A. acuminata* (A.a.) and *Dodonaea inaequifolia* (D.i.), at site RO).

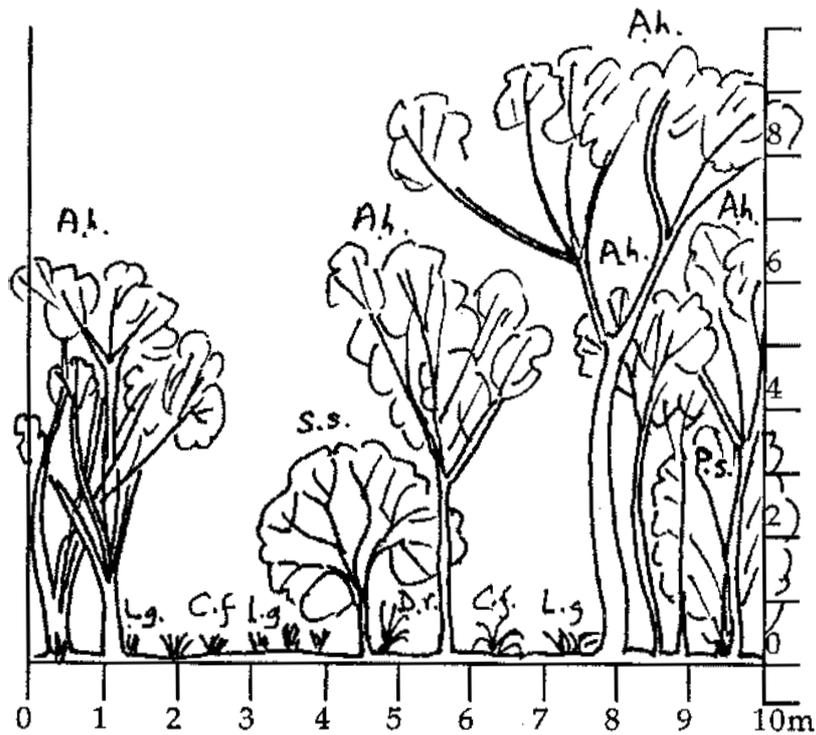


Figure 5. Profile (tree 24; ht 330 cm, stand of *Santalum spicatum* (S.s.) with *Allocasuarina huegeliana* (A.h.), *Chamaexeros fimbriata* (C.f.), *Dianella revoluta* (D.r.), *Lepidosperma drummondii* (L.d.), and *Persoonia striata* (P.s.) at site RE).

localities where more than two thirds of sandalwood have it nearby. The R locality has fewest *A. acuminata* with none at RS and RE. When *A. acuminata* is absent then *Dodonaea inaequifolia* and *Alyxia buxifolia* are present at PA and *Allocasuarina huegeliana* at CK3B. At RO, *D. inaequifolia* is also important (Fig 4); at RE *A. huegeliana* dominates (Fig 5); at RS and R both *Dodonaea viscosa* and *Leptospermum erubescens* are the main shrubs present. *Acacia colletioides*, *A. hemiteles* and *A. erinacea* are only important as associates of *S. spicatum* at PA, the woodland locality.

Not all species listed in Table 2 are likely to be valuable as host plants to sandalwood and the 8 species listed once only may be assumed to be chance co-occurrences. For example, *Eucalyptus crucis* is common at SRNR at rock edges but there is only one joint occurrence with sandalwood. Similarly 5 other species from locality R, including *Persoonia striata* (Fig 5), occur once with sandalwood. Some 27 species co-occur with sandalwood at a frequency of 5% or less. Sandalwood is more often found adjacent to many of these species rather than within patches of them. Thus, sandalwood does not occur under trees of *Eucalyptus capillosa*, that, similar to the related *E. wandoo* Blakely, tend to lack a shrub understorey (Lamont 1985). Many of the sandalwood with either *Eucalyptus loxophleba* or *E. capillosa* also have *Acacia acuminata* present. Relatively poor crowns of *A. acuminata* (e.g. CK3B) compared with the same species where *S. spicatum* is absent, suggest it is damaged by the parasite.

Of the thicket species, *Leptospermum erubescens* is highest up the list. Sandalwood does not occur within dense thickets of this species, rather to the edge. The thicket (or broom bush) habit of most *Melaleuca* species, and of *Allocasuarina campestris* and *Calothamnus asper* (important at CK3), may hinder the development of *S. spicatum* as it is not found directly under shade (Figs 4, 5).

### Reproductive efficiency

Flowering has been observed regularly in March but the intensity of flowering on particular individuals does not seem to be related to the size of the following nut crop. In March 1994, 50 sandalwood trees at 3 localities were examined for freshly fallen nuts from the 1993 season. Thirty six trees (72%) had 174 ( $\pm$  se 36) nuts and 14 had none. Of these 36, 14 of 27 examined in March 1995, (i.e. 52%), had 83 ( $\pm$  se 36) nuts and 13 had none (9 were not examined). Thirty three of the same 36 trees were examined in March 1996 when 29 (88%) had 80 ( $\pm$  se 18) nuts.

In March 1995, a total of 76 trees at 3 localities was examined for nuts from the 1994 season. Thirty seven (49%) had 56 ( $\pm$  se 15) nuts and 39 had none. In March 1996, 139 trees from 4 localities were examined for nuts from the 1995 season. Ninety seven (70%) had 149 ( $\pm$  se 36) nuts and 42 had none.

There are significant differences by locality for the 36 trees with fruit from the 1993 season ( $F = 6.371$ ;  $P = 0.005$ ). Those at CK3 had more nuts ( $369 \pm$  se 101;  $n = 9$ ) than at PA (mean  $118 \pm$  se 36;  $n = 14$ ) and R ( $100 \pm$  se 36;  $n = 13$ ). The latter two do not differ significantly. Differences are not significant for those of the 36 that also fruited in 1994; CK3,  $82 \pm$  se 19 ( $n = 2$ ); PA,  $24 \pm$  se

12 ( $n = 4$ ); R,  $112 \pm$  se 61 ( $n = 8$ ); or 1995; CK3,  $105 \pm$  se 52 ( $n = 6$ ); PA,  $100 \pm$  se 34 ( $n = 11$ ); R,  $49 \pm$  se 17 ( $n = 12$ ).

Mean nut numbers differ significantly by locality for the 76 examined in 1995 ( $F = 4.137$ ;  $P = 0.02$ ). Those at R have most ( $68 \pm$  se 32;  $n = 16$  of which 13 had nuts and 3 did not). The other 2 sets have significantly fewer nuts: CK3,  $22 \pm$  se 7 ( $n = 36$ ), of which 17 had nuts and 19 did not; PA,  $9 \pm$  se 4 ( $n = 24$ ), 7 with and 17 without nuts. Those with nuts ( $\Sigma n = 37$ ) have 83 (R); 46 (CK3); and 31 (PA) with  $\pm$  se of 38, 12 and 8 respectively. These means do not differ significantly ( $F = 0.992$ ,  $P = 0.381$ ).

Significantly more nuts ( $F = 3.806$ ;  $P = 0.012$ ;  $\Sigma n = 139$ ) are again found for 1996 (from the 1995 fruit season) for R trees ( $258 \pm$  se 110,  $n = 29$ , of which 28 had nuts), when trees are compared for each of the 4 localities. The trees from CK3B ( $96 \pm$  se 38,  $n = 34$ , of which 31 had nuts), PA ( $88 \pm$  se 21,  $n = 32$ , of which 28 had nuts), and CK3 ( $20 \pm$  se 9,  $n = 44$  of which 10 had nuts) do not differ in nut numbers. Those with nuts ( $\Sigma n = 97$ ) have means of 267 (R); 106 (CK3B); 100 (PA); and 88 (CK3) with  $\pm$  se of 113, 41, 23 and 31 respectively. These means do not differ significantly ( $F = 1.461$ ,  $P = 0.230$ ).

Numbers of nuts below trees from the 1995 crop are highly correlated with each of 1996 measures of mean crown diameter (CD), tree height (Ht) and stem diameters (SD 5, 15 or 130 cm). For example, of the 34 trees at CK3B correlation coefficients are as follows; SD at 130 cm,  $r = 0.738$  ( $P = 0.001$ ); CD,  $r = 0.625$  ( $P = 0.001$ ); Ht,  $r = 0.597$  ( $P = 0.01$ ); SD 5 cm,  $r = 0.488$  ( $P = 0.01$ ); and SD 15 cm,  $r = 0.374$  ( $P = 0.05$ ).

Division of CK3B trees into 2 sets based on height  $>$  or  $<$  300 cm shows that for 15 larger trees ( $>300$  cm tall, mean  $383 \pm$  se 21 cm) the nut number per tree is 176 ( $\pm$  se 81). Nuts are correlated with tree dimensions as follows; SD 130 cm,  $r = 0.780$  ( $P = 0.001$ ); Ht,  $r = 0.698$  ( $P = 0.001$ ).

**Table 3**

Statistics for numbers of nuts counted on 10 trees of Locality R in each of 1994, 1995 and 1996.

SET	Tree	Tree height (cm) in 1996	Number of nuts counted in		
			1994	1995	1996
R	1	225	191	500	50
R	30	324	480	215	216
RS	16	158	28	3	18
RS	17	178	30	7	45
RS	18	161	8	2	20
RS	19	130	0	0	0
RE	25	273	172	19	33
RE	24	330	160	40	23
RE	22	311	42	111	15
RE	23	167	7	0	10
	Mean	226	112	90	43
	se	24	47	51	20
	F =	5.049	7.624	13.386	4.691
	P =	0.044	0.018	0.004	0.051
Means	R	275 <sup>a</sup>	336 <sup>a</sup>	358 <sup>a</sup>	133 <sup>a</sup>
	RS	157 <sup>b</sup>	17 <sup>b</sup>	3 <sup>b</sup>	21 <sup>b</sup>
	RE	270 <sup>a</sup>	95 <sup>b</sup>	43 <sup>b</sup>	20 <sup>b</sup>

superscript letters indicate significant differences within columns, by LSD test.

= 0.01); CD,  $r = 0.674$  ( $P = 0.01$ ); SD 5 cm,  $r = 0.525$  ( $P = 0.05$ ); but not SD 15 cm,  $r = 0.284$  (NS). For the 19 smaller trees (<300 cm tall,  $237 \pm \text{se } 11$  cm) the nut number per tree is  $34 (\pm \text{se } 10)$  and nut numbers are correlated only with CD,  $r = 0.732$  ( $P = 0.001$ ). Other values are; Ht,  $r = -0.034$  (NS); SD 15 cm,  $r = 0.398$  (NS); SD 5 cm,  $r = 0.164$  (NS); and SD 130 cm,  $r = 0.029$  (NS).

At locality R, 1996 nut numbers vary from 1 to 2 500. Despite considerable variation, there is no significant difference in 1996 nut counts between the four sub-sets of R ( $F = 1.653$ ;  $P = 0.203$ ). The following summarises 1996 counts; set R,  $n$  with nuts =  $8\ 351 \pm \text{se } 308$ , range 1–2 500; set RO,  $n = 7$ ,  $603 \pm \text{se } 259$ , range 20–2 000; set RE,  $n = 9$ ,  $28 \pm \text{se } 9$ , range 8–77; set RS,  $n = 5$ ,  $40 \pm \text{se } 11$ , range 18–80.

Nut records are incomplete for the 3 year period but the available yields from 10 trees of locality R reveal significant differences between sets for each year (Table 3). RS trees are of smaller stature, yield fewest nuts, occur very close to rock (tree 19 is in a fissure) and have *Dodonaea viscosa* or *Lepidosperma* sedges as closest associates. Trees at R are taller, yield most nuts, occur in a range of distinctive habitats and of the two listed one is associated with *Acacia acuminata* and *Allocasuarina huegeliana*, the other with *Leptospermum erubescens* and *Dodonaea viscosa*. Trees at RE occur with *Allocasuarina huegeliana*, *Dodonaea viscosa* or *Leptospermum erubescens*. These 10 indicate a decline in nut production over the 3 seasons, although only 4 trees give largest yields for the 1993 fruit season and 3 have highest yields from the most recent season.

Consideration of the 1996 nut assessment ( $n = 97$ ) suggests that quantity of nuts is extremely variable but the larger trees have more. The best fit of nuts with tree dimension is the exponential relationship;

$$\text{nuts} = 3.914 \times 10^{(0.00364 \text{ CD})}$$

( $r^2 = 0.316$ ; Fig 6).

**Seedlings**

Sandalwood seedlings are present at each locality, with a mean stocking per ha of 39.8, excluding the diffuse set R (Table 1). Seedlings are not present with all trees e.g. on the rockier sites (R) no seedlings are present at either RE or RS. Seedlings are currently only found near or directly underneath putative parent trees. At

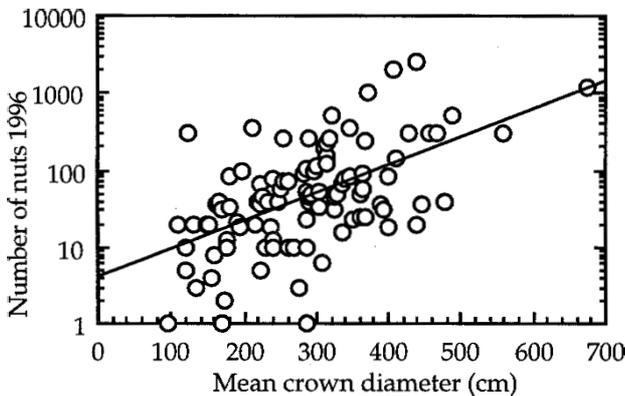


Figure 6. 1996 nut production and mean crown diameters.

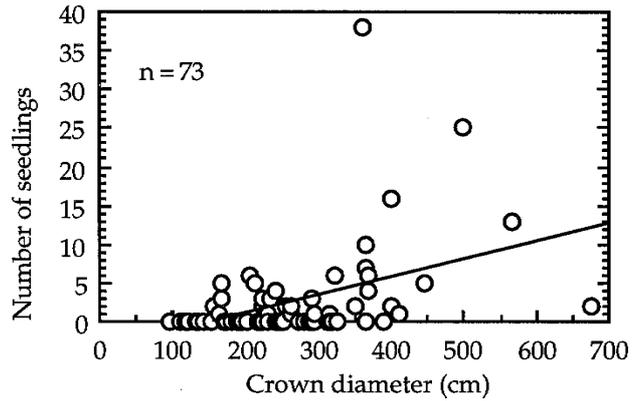


Figure 7. Relationship between seedling numbers and crown diameter of parent trees for  $n = 73$  at localities PA and CK3B combined. Seedlings =  $-3.539 + 0.02304$  Crown diameter (cm);  $r^2 = 0.180$ .

locality PA, 1996 seedling numbers near measured trees are correlated with the 1996 nut count ( $n = 32$ ,  $r = 0.805$ ,  $P = 0.001$ ) and with soil depth ( $r = 0.385$ ,  $P = 0.05$ ). In contrast, at CK3B, seedlings are correlated with sandalwood height ( $n = 34$ ,  $r = 0.367$ ,  $P = 0.05$ ) and SD 15 cm ( $r = 0.398$ ,  $P = 0.05$ ). Lumping PA and CK3B observations ( $n = 73$ ) suggests that crown diameter is the best predictor of seedling numbers ( $r = 0.424$ ,  $P = 0.001$ ). Figure 7 illustrates the relationship described by the regression;

$$\text{seedlings} = -3.539 + 0.02304 \text{ crown diameter (cm)}$$

$r^2 = 0.180$  ( $n = 73$ ,  $P < 0.001$ ). If trees with no seedlings are excluded, then the regression is not significant;

$$\text{seedlings} = -0.9566 + 0.02164 \text{ crown diameter (cm)}$$

$r^2 = 0.111$  ( $n = 31$ ,  $P$  is NS).

At CK3B, the 119 seedlings represent a mean of  $3.5 (\pm \text{se } 1.2)$  per tree ( $n = 34$ ). However, 12 trees have no seedlings, those 22 with seedlings have 1–38 present with  $5.4 (\pm \text{se } 1.7)$ . Sixteen sandalwoods have 1–5 seedlings each, accounting for 73% of all seedlings. The largest numbers per tree are associated with tree 26 (38 seedlings) and tree 11 (16 seedlings). Seedlings associated with the 15 tallest (> 300 cm) trees ( $6.7 \pm \text{se } 2.5$  seedlings) are not significantly correlated with any other observations. Those associated with the 19 shorter (< 300 cm) trees are fewer in number ( $0.9 \pm \text{se } 0.3$ ) and

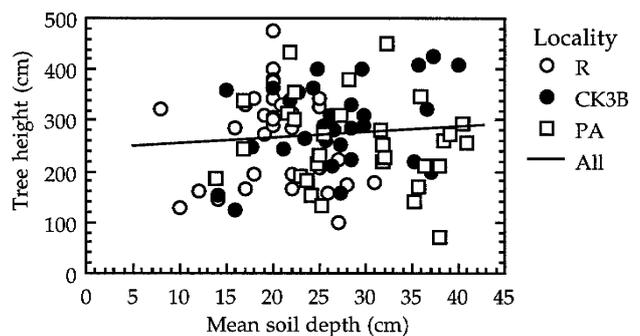


Figure 8. Relationship between tree height and mean soil depth for sandalwood trees.

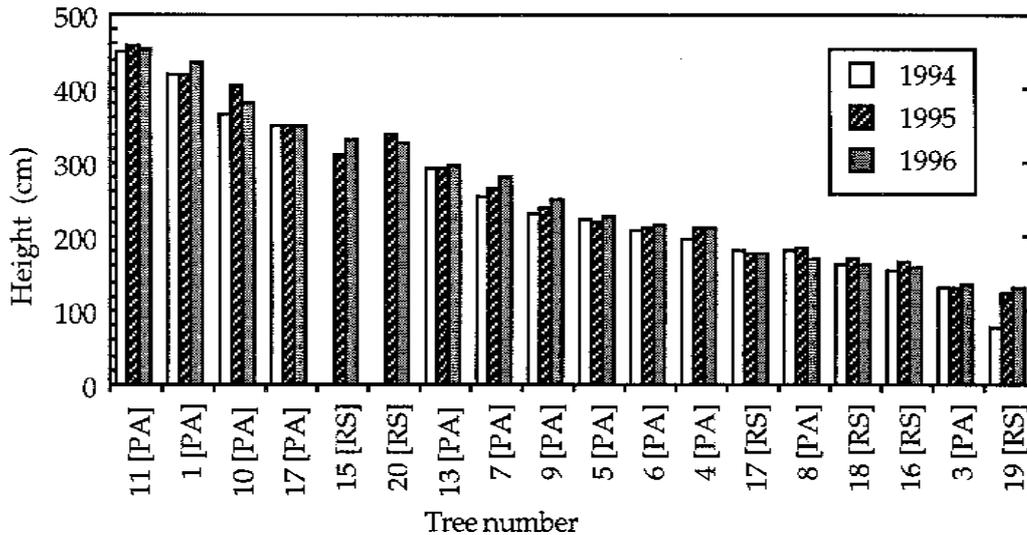


Figure 9. Measured heights for 18 trees 1994–1996 (Sites PA and RS).

only (negatively) correlated with SD 130 cm ( $n = 11$ ,  $r = -0.645$ ,  $P = 0.05$ ).

**Soil**

Large sandalwoods with past high nut production have considerable litter debris beneath the crown. Observation suggests this facilitates growth of introduced annual grasses (*Briza*, *Avena*). Soils are generally sandy loams and mean soil depth taken near sandalwood trees differ significantly between 3 localities (CK3 not available;  $F = 15.510$ ,  $P = 0.001$ ). Soil is deepest at PA ( $28.9 \text{ cm} \pm \text{se } 1.3$ ,  $n = 32$ ), similar at CK3B ( $27.0 \pm \text{se } 1.2$ ,  $n = 32$ ) and significantly shallower at R ( $20.6 \pm \text{se } 0.8$ ,  $n = 36$ ). Mean soil depths at each of the R subsets are similar, between 19 and 21 cm.

Correlation analysis reveals that soil depth is significantly positively correlated with tree height for CK3B trees ( $n = 32$ ,  $r = 0.421$ ,  $P = 0.05$ ). Soil depth is not significantly related to any other dimensions recorded. The linear fit for CK3B trees is;

$$\text{plant height (cm)} = 137 + 6.171 \text{ soil depth (cm)}$$

(1996,  $n = 32$ ,  $r^2 = 0.177$ ). Plant height is negatively

correlated with soil depth for plants immediately adjacent to granite, locality R;

$$\text{plant height (cm)} = 324 - 3.211 \text{ soil depth (cm)}$$

(1996,  $n = 36$ ,  $r^2 = 0.028$ ,  $P$  is NS). A similar, non-significant, relationship occurs with PA trees. When these 3 locality sets are combined (Fig 8) plant height has no correlation with soil depth.

The 15 taller trees ( $> 300 \text{ cm}$ ) at CK3B have a soil depth of  $28.6 (\pm \text{se } 1.9)$  compared with the 19 trees  $< 300 \text{ cm}$  with  $24.6 (\pm \text{se } 1.5)$ . This difference is not significant.

**Growth**

Six of the 10 taller sandalwoods (Table 1) are in CK3B, which also has the tallest individual sandalwood. The upper limit to growth is likely to be determined by a combination of site influences and may require a considerable time period for it to be established. Tree architecture in parasitic tree species appears less robust and formalised than in free living species. In sandalwood, growth increments are difficult to detect as foliage is brittle and easily lost to wind, bird damage and fungal infections. This affects height

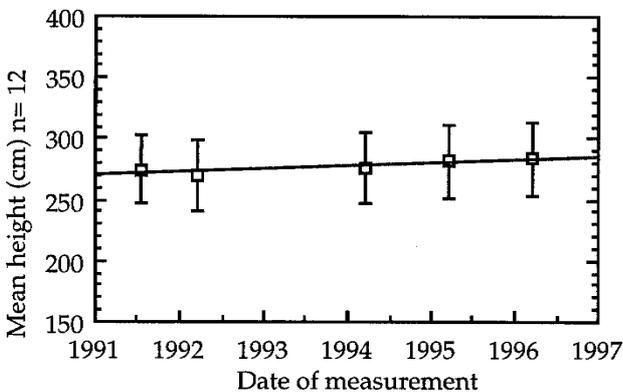


Figure 10. Mean heights and standard errors for 12 trees consistently measured at locality PA.

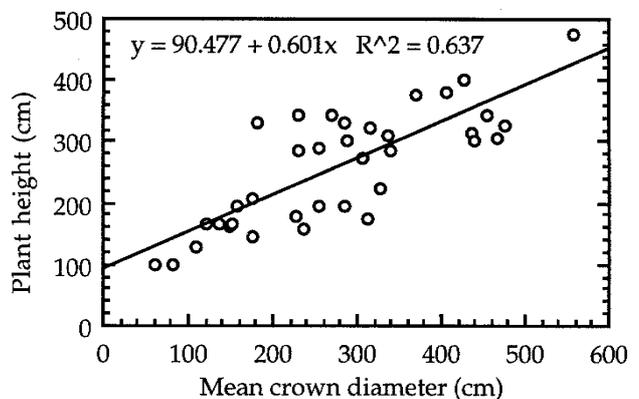


Figure 11. Relationship between plant height and crown diameter for plants immediately adjacent to granite (1996,  $n = 36$ ).

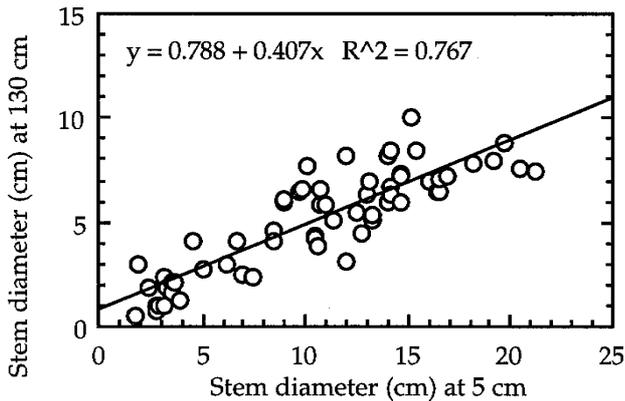


Figure 12. Relationship between stem diameters at 130 and 5 cm for measured trees at locality CK3 (two large outliers removed).

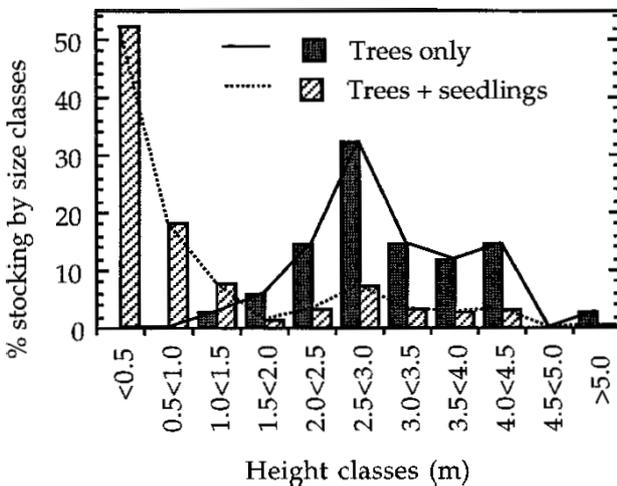


Figure 13. Sandalwood stocking March 1996 at CK3B, with and without seedlings.

and crown estimates. From year to year changes may be subtle (Fig 9) although seedling growth may be more easily recorded. For tree heights at least five years is necessary for reasonably robust estimates of change to be detected (Fig 10).

Tree architecture tends to be characteristic with some populations having a distinct main trunk, albeit not very long; others are shrubby with multiple branches from a metre or so. The characteristics of mature populations are revealed by correlations between dimensions. For example there is usually a consistent and reliable relationship between plant height and crown diameter (Fig 11) and between the several measures of stem diameter (e.g. Figure 12).

The problem of assessing population dynamics in relation to seedling establishment is important. Figure 13 indicates that seedling populations can be considered separately from that of trees or can be considered together with trees. Thus far, no seedling populations have been encountered away from mature trees.

## Discussion

On granite exposures of the Darling scarp above Perth, the Christmas tree *Nuytsia floribunda* (Labill) R Br is common and may have a similar role in vegetation (Lange 1960) to that of the sandalwood described here. Sandalwood does not have the same ability to persist through suckering and populations may have greater genetic diversity than in *N. floribunda* or than *Santalum album* L which can sucker profusely. The phenomenon of clumping with individuals of seed origin may render populations more robust. However, some autoparasitism must occur amongst the several dense seedling clumps and this may reduce growth. Highest apparent densities are at localities adjacent to granite but areas sampled are comparatively small. Sandalwood clumping involves both large individuals and seedlings occurring in close proximity. Ultimately this results from poor seed dispersal. The large fruits appear not to be currently taken by emu (*Dromaius novaehollandiae* Latham) although evidence of its presence is seen frequently with scats heavily loaded with seed of *Eremophila ionantha*.

Continuous regeneration is suggested by seedling densities but is at present confined to clumps. R trees show greatest departure from a normal distribution with two peaks; this may have more to do with the variation in habitats encompassed than to past recruitment periods. Seedling presence near parent trees may reflect current rabbit pressure. It will be interesting to observe whether rabbit decline following the calcivirus virus coincides with sandalwood seedlings establishing further away from parent trees.

The distribution of sandalwood at SRNR reveals the circumstances in which it is able to persist. It is absent from pure stands of the larger eucalypt trees e.g. *Eucalyptus capillosa*, *E. salmonophloia* F Muell and *E. salubris* F Muell, presumably as these dominate their edaphic environments and may allow insufficient light for sandalwood. Competition for soil moisture in dry weather is the main factor limiting the stocking of large trees that can be supported in such stands. The taller woodlands are confined to areas of deeper soils with limited stands of salmon gum (*E. salmonophloia*) forming the tallest woodland stratum. Although sandalwood is absent with this species, *Santalum acuminatum* is able to occur (Keenan 1993). Sandalwood can persist in the vicinity of York gum mallee; this species is frequently in small patches that border *Acacia* and *Leptospermum erubescens* thickets.

Plant parasites can attack many hosts and can use multiple hosts simultaneously (Musselman & Mann 1978; Gibson & Watkinson 1989). A single *S. spicatum* may parasitise variable numbers and species of hosts (Herbert 1925). It is assumed that plants frequently with sandalwood are both good hosts and good survivors. Hosts that cause best parasite performance may suffer more from parasitism and there will be some upper limit to the amount of parasites that can be tolerated by particular host communities.

Whereas host preferences of epiphytic parasites can be observed directly, those of root parasitic trees can only be inferred without exploring root connections (Pennings & Callaway 1996). Pot trials with host/parasite pairs suggest direct negative effects on host

growth (Marvier 1996) and that growth is better when associated with some hosts rather than others (Rai 1990; Fox *et al.* 1996; Marvier 1996). Six of those listed are noted by Loneragan (1990) as host species; *Acacia acuminata*, *A. colletioides*, *A. hemiteles*, *Cassia nemophila*, *Eucalyptus loxophleba* and *E. capillosa*. The jam tree *Acacia acuminata*, the lily *Dianella revoluta*, the medium shrub *Dodonaea inaequifolia* and the tree *Allocasuarina huegeliana*, as the most frequent associates of *Santalum spicatum* at SRNR, are likely the best hosts. All except *D. inaequifolia* are present at the successful sandalwood plantation at Dryandra (Struthers *et al.* 1986) and Loneragan (1990) has indicated another *Dodonaea* (*D. lobulata* F Muell) as an important host. A species listed by Loneragan (1990) that does not feature in Table 2 is *Eremophila ionantha* (Diels) in Diels & E Pritzel. This is common at SRNR as an understorey species in eucalypt stands.

Species listed by Loneragan (1990) that are probably not important hosts with *S. spicatum* near granite areas at SRNR are; *Acacia colletioides* and *A. hemiteles*, and the eucalypts *E. loxophleba* and *E. capillosa*. These *Acacia* species, and *A. erinacea*, are associated with salmon gum (Fox *et al.* 1993) and only occur as associates of *S. spicatum* at PA, the woodland locality on slightly deeper soils. Other *Acacia* species of this reserve are confined to sandier soils where *S. spicatum* is entirely absent (e.g. *A. stereophylla*, *A. neurophylla* W Fitzg, *A. coolgardiensis* Maiden). Other evidence (Fox, unpublished) suggests that eucalypts generally are poor hosts and this is generally associated with competition for soil moisture (Lamont 1985). *Allocasuarina campestris*, *Melaleuca hamulosa* and *M. lateriflora* form thickets to < 3 m (Fox *et al.* 1993) and sandalwood does not occur amongst stands of these or of *Calothamnus asper*. Some overhead light appears necessary to support sandalwood growth. Loneragan (1990) listed *Casuarina cristata* Miq and *Dodonaea lobulata* F Muell, as hosts. These species are not found at SRNR but it is postulated that species in these genera (and *Allocasuarina*) are likely to be universally good hosts for sandalwood. The tree *Allocasuarina huegeliana* is of considerable interest as it provides the greatest standing biomass over much of the distribution of *S. spicatum* and, presumably, also the greatest volume of available roots for haustorial connections; *A. huegeliana* is often the dominant species of rockier areas. The frequency of occurrence of the perennial lily *Dianella revoluta* suggests that this species is probably utilised as a host by sandalwood. Earlier circumstantial evidence linking *D. revoluta* to sandalwood at Dryandra is alluded to by Struthers *et al.* (1986).

Low or sporadic fruit set is common in semi-parasites (Musselman & Mann 1978). Contrary to perceived belief (Loneragan 1990; Kealley 1991), sandalwood trees are regular in flowering. Flowering is more likely a photoperiodic response than one to rainfall, as buds invariably open at SRNR between February and May. The quantity of flowers, duration of flowering, fruit set and maturation are all variable and may depend on seasonal rainfall, prior fruiting history and tree size. Up to 700 flowers may result in only one fruit (Barrett 1987). Nut production is irregular (Davies 1976) and differs between trees and seasons. There is considerable range in yield with 2 000 to 2 500 nuts recorded from some larger trees. The proportion of trees fruiting in 1993 and

1995 is similar, and higher than in 1994. Similarly, the number of nuts per tree on those fruiting is lowest from the 1994 season. Of trees observed to have fruited in 1993 and also examined subsequently, mean nut production from the 1994 and 1995 seasons is about half that from 1993, and the lowest proportion of trees fruited again in 1994 compared with 1995. Significant differences in nut production between trees at different localities tend to be lost when trees barren in that year are not included in the analysis. However, it is of interest that trees at the more northern location produced most fruit per tree in the 1993 season whereas some trees from the rockier localities produced more nuts from both the 1994 and 1995 seasons.

Nut production from taller trees (> 300 cm height) is correlated with several dimensions of plant size, all reflecting age and relative maturity, but for smaller trees nut yield is only related significantly with crown diameter. This suggests that crown spread has more influence on nut yield than stem size or tree height.

Nut weight and diameter in *S. spicatum* differs in relation to longitude (Fox & Brand 1993), mainly associated with falling away of mean rainfall inland. Some trees located adjacent to granite may have higher effective soil moisture available in the fruit forming winter months due to redistribution. This may have an influence on the size of the nut crop. The massive loss of flowers (Barrett 1987), large nut size (Musselman & Mann 1978; Fox & Brand 1993), poor germination (Loneragan 1990) and brittle foliage suggests low resource efficiency is a physiological consequence of parasitism.

Regeneration of dominants is uncommon. Release from canopy held seed in eucalypts may compensate for irregular fruiting (Yates *et al.* 1994) but there is no such effect in sandalwood. The availability of viable seed may limit seedling regeneration and this is a topic for further research. Concern has been expressed that seedling regeneration of sandalwood is retarded by herbivore activity. Until 1996 rabbits and kangaroos were frequently seen at SRNR. A viral disease reduced kangaroo numbers in the summer of 1995–96, and rabbit numbers appear to fluctuate with myxoma virus outbreaks. It is possible that saturation of space under parents by nut material may have deterred rabbit herbivory. With the introduction of the calici virus it is possible that the next few years may see increased sandalwood regeneration, away from parent trees.

In the terminology used by other speakers at this symposium, some sites near granite outcrops may be termed as apron or petticoat places. These have shallow or poorly developed soils unable to support perennial species. Other sites lie in long narrow gaps between large rounded sections of granite where deeper or more developed soils do support perennials. Sandalwood is rarely found at such sites occupied by *Eucalyptus crucis*; these narrow garter sites lie at areas where the steeply shelving rock appears to dive beneath the regolith such that organic matter has accumulated and where soil moisture may be comparatively high. In supporting this long-lived eucalypt the sites may be too dry in summer to support sandalwood.

It is possible that sandalwood is restricted to relatively nutrient poor sites (Matthies 1995). Soils are sandy loams,

grey and gritty (Muir 1979). Both main tree hosts occur on granitic sandy soils (Lange 1960). However, granitic soils of the region are characteristically high in potassium (McArthur 1991), important in sandalwood nutrition (Struthers *et al.* 1986). The two important host tree species both fix nitrogen; *A. acuminata* (Roughley 1987), *A. huegeliana* (Rodriguez-Barrueco 1968). Best occurrence is often between or adjacent to different vegetation types. Such locations may provide the widest range of hosts (Kealley 1991) as sandalwood root extension is considerable and allow some access to better soils. Sandalwood is not found in very shallow soils but is also scarce in well-developed eucalypt woodlands where soil depth may be much deeper. Light competition coupled with root saturation may restrict it in such areas. Alternatively, present absence may result from lack of regeneration following exploitation last century.

The balance between competitive and host effects is related to growth conditions (Watkinson & Gibson 1988). Do larger parasites directly diminish host growth? *Acacia acuminata* is in poor condition near a number of sandalwood occurrences. Another favoured species, *A. tetragonophylla* (Loneragan 1990) is present, but now scarce, at location PA and may have declined due to sandalwood parasitism. Do host species differ in tolerance of parasitism? *Allocasuarina huegeliana* appears to be more robust than the *Acacia* species, it reaches a large size and probably persists longer. It may not suffer as much from parasitism as *A. acuminata*.

### Conclusions

Hosts function as sources of water and nutrients for the parasite. Potential hosts may offer competition by reducing light available to the parasite. *Santalum spicatum* appears better able to occur adjacent to the lighter shade cast by the nitrogen-fixing host trees *Acacia acuminata* and *Allocasuarina huegeliana* than under most eucalypt species. Poor crown condition of *A. acuminata* near *S. spicatum* indicates that the parasite damages at least this host. It is considered that the particular edaphic environments that permit the development of the recognised host tree species of *Acacia acuminata* and *Allocasuarina huegeliana* to flourish are mainly responsible for the prolific occurrence of *Santalum spicatum* at Sandford Rocks Nature Reserve. It is possible that most species of *Dodonaea* are likely hosts for sandalwood.

The commercial size for harvest of sandalwood is a trunk diameter of > 127 mm measured at 150 mm from ground level (Keally 1991). A number of trees in the populations at SRNR exceed this criterion.

Evidence is presented to demonstrate that there is no shortage of seedlings of *Santalum spicatum* in an environment where rabbits have been abundant. At the seedling stage sandalwood is shade tolerant but no mature trees occur under overhead shade. Four growth stages are postulated from the evidence produced;

- 1) initial establishment of small seedlings (1–2 years from seed);
- 2) persistence as seedling-sapling to ca 1 m height (2–8 years);
- 3) growth to mature size 2.5–3.5 m (10–30 years);

- 4) continued growth in stem diameter and crown spread, little change in height (30–100 years).

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