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Intermediate host influences on the root hemi-parasite *Santalum album* L. biomass partitioning

Andrew M. Radomiljac[a,b,*], Jen A. McComb[b], John F. McGrath[a]

[a] *Department of Conservation and Land Management, CALM Science, Locked Bag 104, Bentley Delivery Centre 6983, Australia*
[b] *Division of Science, Biological Sciences, Murdoch University, Perth, 6150, Australia*

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Abstract

Santalum album L. seedlings parasitised on the N_2-fixing woody hosts *Sesbania formosa* (F. Muell.) N. Burb., *Acacia trachycarpa* E. Pritzel and *A. ampliceps* Maslin and the non-N_2-fixing woody host *Eucalyptus camaldulensis* Dehnh. were grown for 38 weeks in 25 l nursery containers. *S. album* growth was greater and root : shoot ratio lower for *S. album* seedlings grown with N_2-fixing hosts compared with seedlings grown with *E. camaldulensis* or with no host. Seedlings grown with *S. formosa* had a greater stem diameter, height, leaf area, root and shoot dry weight (DW) than all other treatments. *S. album* grown with *S. formosa* and *A. ampliceps* had a lower root : shoot ratio than all other treatments at all assessments. The root : shoot ratio of unattached *S. album* increased exponentially over the 38 week period. Seedling growth declined for all treatments between the 33 and 38 week harvests, except for those seedlings attached to *A. trachycarpa*. A strong positive linear relationship was shown between *S. album* leaf area and shoot DW irrespective of host species. No relationship was found between *S. album* shoot DW and root : shoot ratio with host shoot DW. The combined *E. camaldulensis* and *S. album* root system supported a smaller *S. album* shoot biomass compared with the *S. album* shoot biomass supported by the combined root systems of the N_2-fixing hosts and *S. album*. Compared with all other host species the *A. trachycarpa* root system was more efficient in supporting its own shoot biomass and the total biomass of *S. album*. Host use efficiency (*S. album* shoot DW/host shoot DW) values of *S. formosa* and *A. trachycarpa* were greater than the host use efficiency values of *A. ampliceps* and *E. camaldulensis*. Values for unparasitised *S. formosa* leaf area, shoot and root DW and root : shoot ratio were greater than those for parasitised plants.

Keywords: *Santalum album*; Santalaceae; Root hemi-parasite; Indian sandalwood; Intermediate host; N_2-fixing host; Pot study

1. Introduction

Indian sandalwood is the highly valued aromatic heartwood from the sub-tropical root hemi-parasite *Santalum album* L. Sandalwood utilisation has occurred for 20 to 30 centuries in eastern cultures (Srinivasan et al., 1992) and over exploitation of most natural populations has generated an acute supply shortage (Havel and McKinnell, 1993). Establishment of plantations of *S. album* in northern Western Australia is progressing (Radomiljac, 1998; Radomiljac et al., 1998a). The parasitic requirements of *S. album*

*Corresponding author. Tel.: +61-89-334-0161; fax: +61-89-334-0327; e-mail: andrewr@calm.wa.gov.au

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greatly increases the complexity of plantation silviculture (Radomiljac et al., 1998b).

The single most important silvicultural parameter influencing plantation survival and growth is the host plant. For plantations, host plants are divided into three categories: pot, intermediate and long term hosts (Fox et al., 1996; Radomiljac et al., 1998b). The function of the pot host has been described (Radomiljac et al., 1998a). In northern Western Australia the herbaceous *Alternanthera nana* R. Br. has been shown to be an ideal host as it promotes high *S. album* survival and growth following field establishment (Radomiljac, 1998). The intermediate and long term hosts are propagated simultaneously in separate nursery containers. At field establishment both host types are strategically placed within the plantation. The intermediate host, usually a fast-growing short-lived perennial, acts as a 'bridging agent' between the pot host and long term host and should promote early *S. album* plantation growth. Intermediate hosts eventually die or becomes less important following *S. album* attachment to the long term host, which should persist as final host for the entire rotation length.

A number of studies on softwood species have shown a positive correlation between early growth rates and the extent of future heartwood production (Hillis and Ditchburne, 1974; Hillis, 1987; Wilkes, 1991; Climent et al., 1993). Hillis and Ditchburne (1974) showed *Pinus radiata* Donn. trees with the most rapid growth in the first five years had the greatest heartwood diameter at all future ages.

It is important to determine if high early stem growth is positively correlated to high future *S. album* heartwood production as if so, the intermediate host is an extremely important silvicultural component being effective during the early phase of plantation growth.

Despite the importance of the *S. album* : host relationship on *S. album* plantation productivity, the relationship between growth and carbon allocation between the root hemi-parasite and its woody hosts has not been fully resolved (Nayar et al., 1988; Subbarao et al., 1990). Surprisingly little literature exists on the host influences on *S. album* biomass partitioning under controlled conditions. Growth studies on root hemi-parasites have concentrated almost exclusively on the economically important agricultural weeds, such as Orobanchaceae (*Orobanche* or broomrape) and Scrophulariaceae (*Striga* or witchweed) (Press and Stewart, 1987; Graves et al., 1989; Sauerborn, 1991; Graves, 1995) or species which have no economic importance, such as *Olax phyllanthi* (Labill) R. Br. (Tennakoon and Pate, 1996). Scant literature exists on experiments designed to promote growth of root hemi-parasites.

This paper examines the effect of intermediate woody hosts on the growth of *S. album* seedlings and the null hypothesis tested is that *S. album* growth is not enhanced when attached to legume intermediate hosts.

2. Methods

The effect of intermediate hosts on the growth of pot cultured *S. album* seedlings was studied in the Department of Conversation and Land Management's nursery at Kununurra (lat 15°46′ S. long 128°44′ E), Western Australia. The experiment comprised five *S. album*: intermediate host species single plant pairings (intermediate host plants were: *Sesbania formosa* (F. Muell.) N. Burb, *Acacia trachycarpa* E. Pritzel, *Acacia ampliceps* Maslin, *Eucalyptus camaldulensis* Dehnh. and a no host control)×three harvests (24, 33 and 38 weeks after the placing of *S. album* and the intermediate host together in pots)×eight replicates in a randomised complete block design.

In July 1996, 200 uniform *S. album* seedlings (height; 40.5±2.98 cm and basal diameter 3.9±0.58 mm) about six months old growing in 1.4 l pots with *Alternanthera nana* as a pot host, were selected. *S. album* seedlings were propagated following Radomiljac (1998). The *A. nana* was cut to soil level and the *S. album* seedling transplanted to 25 l pots of coarse river sand : peat : perlite at 3 : 2 : 2. Pots were placed on mesh benches 10 cm above ground to avoid root contamination between treatments. A single intermediate host seedling inoculated with *Rhizobium* where appropriate (Table 1) was transplanted to the pot and positioned ca. 150 mm from the single *S. album* seedling. Each intermediate host species was also transplanted into an unreplicated pot and remained as an unparasitised control plant. Intermediate host seedlings were propagated following Radomiljac (1998). A slow release fertiliser, Scotts® Osmocote Plus (8-9M) (N 16.0%, P 3.5%, K 10.0%, S 2.4%, Mg 1.2%, B 0.02%, Cu 0.05%, Fe

Table 1
Host plant origins and *Rhizobium* inocula

Host species	Family	CSIRO seedlot no. [a]	Location		*Rhizobium* inoculum strain no. [b]
Sesbania formosa	Papilionaceae (Fabaceae)	18833	Ivanhoe Crossing, WA	Lat 15°41′ S; Long 128°41′ E	PMA 295/2 5/97
Acacia trachycarpa	Mimosaceae	16774	Mt. Lockyer, WA	Lat 22°24′ S; Long 118°47′ E	PMA 469 5/97
Acacia ampliceps	Mimosaceae	18648	N. shore Lake Nongra, NT	Lat 18°10′ S; Long 129°46′ E	PMA 251/1
Eucalyptus camaldulensis	Myrtaceae	15050	Gibb River, WA	Lat 16°30′ S; Long 126°10′ E	—

[a] Commonwealth Scientific and Industrial Research Organisation Forestry and Forest Products, Australian Tree Seed Centre, Canberra.
[b] University of Queensland, Department of Agriculture, St. Lucia.

0.4%, Mn 0.06%, Mo 0.02% and Zn 0.015%) was then applied at 10 g on the surface of each pot. Four weeks later *A. nana* was completely removed from the pots. Seedlings remained in the nursery for a further 10 months in full sun with overhead watering twice daily, for ≈15 min, to near field capacity.

There were four replicates of five pots with each *S. album*: intermediate host treatment and *S. album* without a host within each replicate. All pots with unparasitised hosts were positioned in one replicate. All pots were randomised within each replicate. The position of the replicate and pots within each replicate were randomly changed only twice due to the large pot size and weight.

3. Assessment

Immediately prior to, and 13, 24, 33 and 38 weeks after planting the host and parasite together, *S. album* and host height and diameter at 2 cm were measured.

On weeks 24, 33 and 38 of the association of parasite and host, three pots per treatment were selected on the basis of one seedling equal to, one +1SD and one −1SD of the mean *S. album* diameter. *S. album* and host plants were harvested by cutting the stem at soil level and the shoot partitioned into stem and leaf material. *S. album* and host leaf, stem and root dry weight (DW) was recorded after plant material had been oven dried at 80°C for 48 h. Remaining pots were retained for further study.

Leaf areas of both *S. album* and hosts were determined by passing a leaf sub-sample through a planimeter (Paton Electronic Planimeter, Stepney, S. Aust.). The DW of the sub-sample was then obtained and the leaf area to DW ratio calculated. *S. album* specific leaf area (SLA) was determined from the ratio of *S. album* total leaf area : total leaf DW.

In this paper, we attempt to determine the effectiveness of hosts by examining the partnerships in the following ways:

1. The ratio between the *S. album* shoot DW and the host shoot DW was termed ‘host use efficiency’ (HUE).
2. The total root biomass utilised by the *S. album* shoot includes its own roots as well as the host root system. The ratio between this total root DW and the DW of the *S. album* shoot is termed the ‘host root extension’ (HRE).
3. The total biomass supported by the host root includes its own shoot as well as the roots and shoot of *S. album*. The ratio between the root DW of the host and the total of the host shoot and *S. album* root and shoot DW is termed the ‘host root support’ (HRS).

Growth data were analysed using ANOVA and Tukey’s pairwise *t*-test. All analyses were performed using SYSTAT® statistical software (Systat., 1992). Regressions were fitted using the regression procedure of SYSTAT®.

4. Results

Differences in growth of *S. album* as a result of parasitism of different host species became clear after week 13. The increase in *S. album* height and diameter

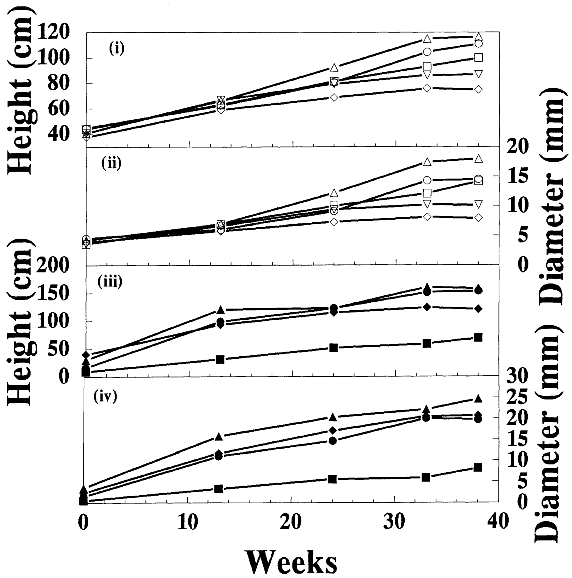

Fig. 1. Growth of *Santalum album* (i) mean height and (ii) mean stem diameter of plants while attached to (△) *Sesbania formosa*, (○) *Acacia ampliceps*, (□) *A. trachycarpa*, (◇) *Eucalyptus camaldulensis* and (▽) no host control. Growth of host species (iii) mean height and (iv) mean stem diameter while parasitised by *S. album*. (▲) *Sesbania formosa*, (●) *Acacia ampliceps*, (■) *A. trachycarpa* and (◆) *Eucalyptus camaldulensis*. Data are from eight replicates. See Table 2 for statistical data.

plateaued between week 33 and 38 except for seedlings attached to *A. trachycarpa* (Fig. 1(i) and (ii)). In relative terms seedlings attached to *S. formosa* showed twice the diameter and thrice the height of seedlings grown with *E. camaldulensis*. A comparison of *S. album* growth 33 weeks after planting the host and parasite together is shown in Fig. 2. Unattached seedlings were consistently larger than those attached to *E. camaldulensis*.

Hosts parasitised by *S. album* increased in height and diameter (Fig. 1(iii) and (iv)). *A. trachycarpa* height and diameter were always significantly lower than all other species.

S. album seedling leaf DW and leaf area increased irrespective of the host species for 33 weeks then declined with the exception of *S. album* attached to *A. trachycarpa*, which continued to increase (Fig. 3). Seedling stem DW remained relatively stable between the harvests at 33 and 38 weeks, except for seedlings attached to *A. ampliceps* and *A. trachycarpa*, which decreased and increased, respectively. Unattached

Table 2
The effects of intermediate host species on *S. album* growth and the growth of intermediate hosts

Dependent variable	Weeks after parasite and host association			
	13	24	33	38
Parasite				
Height	0.004 [a]	0.000	0.000	0.005
Diameter	0.000	0.000	0.000	0.000
Leaf DW	NM [b]	0.000	0.000	0.001
Stem DW	NM	0.002	0.000	0.027
Shoot DW	NM	0.000	0.000	0.006
Root DW	NM	0.028	0.008	0.011
R:S ratio	NM	0.018	ns [c]	0.031
Leaf area	NM	0.001	0.000	0.001
Host use efficiency	NM	0.008	0.000	0.000
S. album+host root: *S. album* shoot ratio	NM	0.008	0.008	0.003
Host shoot+*S. album* plant: Host root ratio	NM	0.002	0.027	0.000
Specific leaf area	NM	0.007	ns	ns
Host				
Height	0.000	0.000	0.000	ns
Diameter	0.000	0.000	0.000	0.002
Leaf DW	NM	0.000	0.000	0.000
Stem DW	NM	0.011	0.000	0.000
Shoot DW	NM	0.002	0.000	0.000
Root DW	NM	0.000	0.001	0.000
R:S ratio	NM	ns	0.024	0.006
Leaf area	NM	0.000	0.000	0.000

[a] Numbers are the probability of no difference in treatment means.
[b] No measurement (NM) taken.
[c] Treatment means are not significantly (ns) different from each other (p>0.05).

seedlings had consistently higher leaf and stem DW and leaf area than seedlings attached to *E. camaldulensis*.

The growth of all parasites and host plant parts was affected by the combination of host and parasite (Table 2). The *S. album* seedling root and shoot DW increased irrespective of the host species treatment up to the harvest at 33 weeks. Root and shoot DW decreased irrespective of the host species treatment between the harvest at 33 and 38 weeks except for *S. album* attached to *A. trachycarpa*, which increased over time. Unattached *S. album* after weeks 24 showed an increase in root DW and a decrease in shoot DW which resulted in an increasing root : shoot ratio over time. The root : shoot ratio of *S. album* grown with *S. formosa* was lower than all other combinations while *S. album* attached

Fig. 2. Growth of the root hemi-parasite *Santalum album* (Sa) after 33 weeks in pot culture with (i) *Sesbania formosa* (Sf), (ii) *Acacia trachycarpa* (At), (iii) *A. ampliceps* (Aa), (iv) *Eucalyptus camaldulensis* (Ec) and (v) no host. Rule is 1 m.

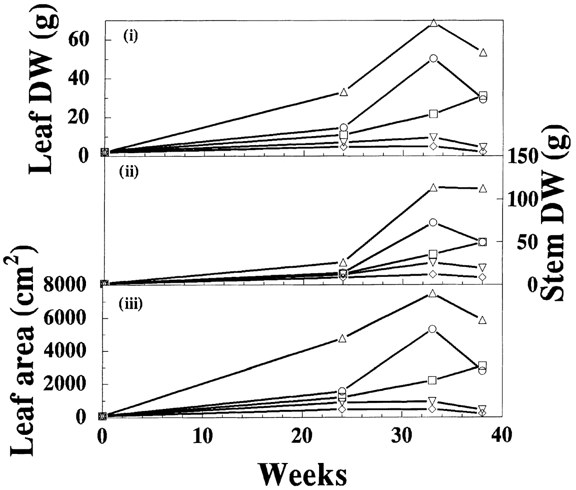

Fig. 3. Growth of *Santalum album* (i) mean leaf dry weight (DW), (ii) mean stem DW and (iii) mean leaf area while attached to (Δ) *Sesbania formosa*, (○) *Acacia ampliceps*, (□) *A. trachycarpa*, (◇) *Eucalyptus camaldulensis* and (∇) no host. Host and parasite associations were grown as single plant pairings in 25 l pots under nursery conditions. Data are from three replicates. See Table 2 for statistical data.

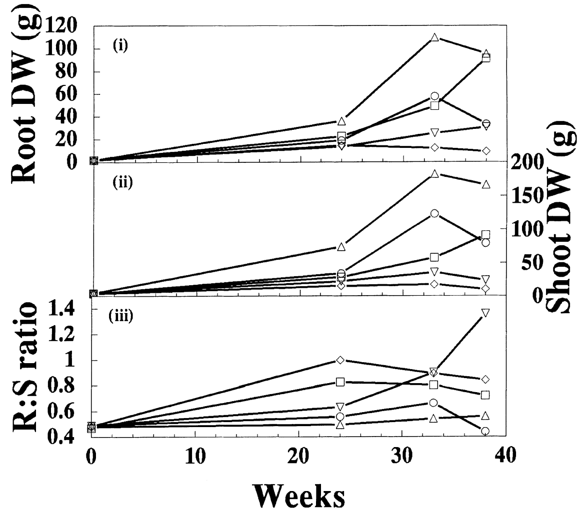

Fig. 4. Growth of *Santalum album* (i) mean root dry weight (DW), (ii) mean shoot DW and (iii) mean root : shoot ratio while attached to (Δ) *Sesbania formosa*, (○) *Acacia ampliceps*, (□) *A. trachycarpa*, (◇) *Eucalyptus camaldulensis* and (∇) no host. Host and parasite associations were grown as single plant pairings in 25 l pots under nursery conditions. Data are from three replicates. See Table 2 for statistical data.

to *E. camaldulensis* had the highest root : shoot ratio over time (Fig. 4).

The impact on biomass partitioning of parasitism on different host species is most clearly seen in week 38 (Fig. 5). The proportion of DW in stems was similar for *S. album* attached to *S. formosa* and *E. camaldulensis* or when grown without a host, but the proportion of DW in roots was least when in association to *S. formosa* and greatest with no host. The DW of leaves showed the opposite trend. Due to this relationship the root : shoot ratios of seedlings attached to *E. camaldulensis* and unattached seedlings were more than double that of seedlings attached to *S. formosa* (Fig. 4(iii)).

Leaf and stem DW and leaf area of parasitised *S. formosa* and *E. camaldulensis* declined over time, whereas the leaf and stem DW and leaf area of *A. trachycarpa* and *A. ampliceps* increased slightly (Fig. 6). The leaf DW, stem DW and leaf area of unparasitised *S. formosa* were reduced by parasitism. Data for unparasitised hosts are only shown for *S. formosa* at week 33.

Root and shoot DW increased for all host species between the 24 and 33 week harvests (Fig. 7(i) and (ii)). Parasitised *S. formosa* and *E. camaldulensis* root and shoot DW declined between the 33 and 38 week harvests whereas *A. trachycarpa* and

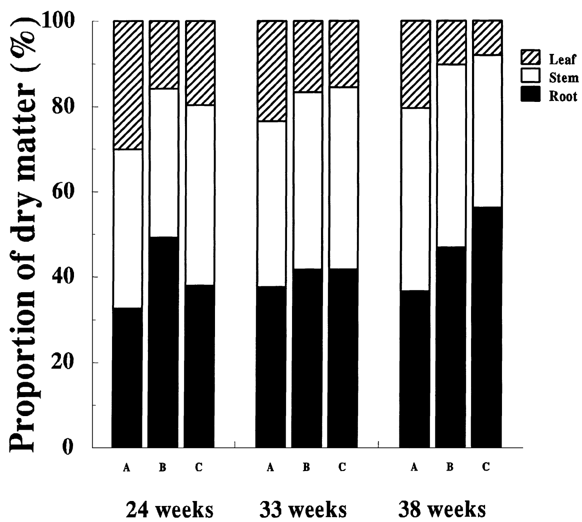

Fig. 5. The proportion of the total *Santalum album* dry weight from leaf, stem and root while attached to (A) *Sesbania formosa*, (B) *Eucalyptus camaldulensis* and (C) no host.

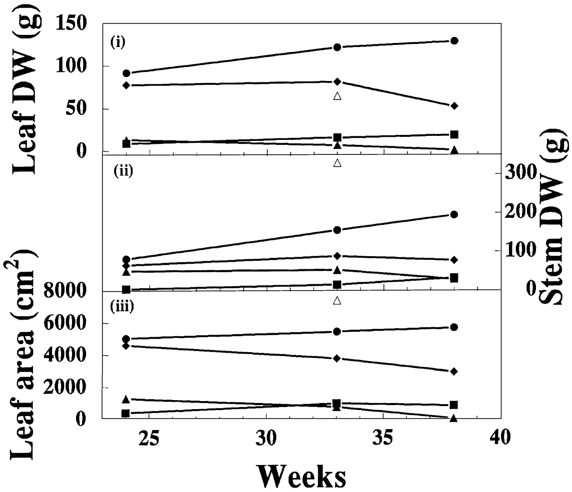

Fig. 6. Growth of host species (▲) *Sesbania formosa*, (●) *Acacia ampliceps*, (■) *A. trachycarpa*, (◆) *Eucalyptus camaldulensis* (i) mean leaf dry weight (DW), (ii) mean stem DW and (iii) mean leaf area while parasitised by *Santalum album* and (△) unparasitised *S. formosa* at the 33 week harvest. Parasitised host and unparasitised *S. formosa* data are from three and one replicates, respectively. See Table 2 for statistical data.

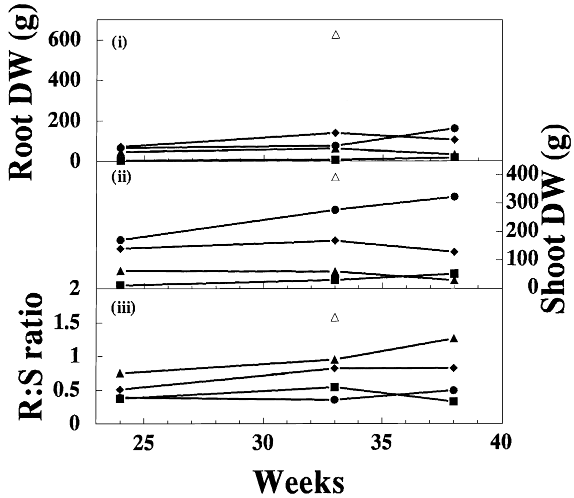

Fig. 7. Growth of host species (▲) *Sesbania formosa*, (●) *Acacia ampliceps*, (■) *A. trachycarpa*, (◆) *Eucalyptus camaldulensis* (i) mean root dry weight (DW), (ii) mean shoot DW and (iii) mean root : shoot ratio while parasitised by *Santalum album* and (△) unparasitised *S. formosa* at the 33 week harvest. Parasitised host and unparasitised *S. formosa* data are from three and one replicates, respectively. See Table 2 for statistical data.

A. ampliceps root and shoot DW continued to increase. *A. trachycarpa* root DW remained constantly lower than the other host species. *S. formosa* root : shoot ratio increased exponentially over time remaining constantly higher than the other host species (Fig. 7(iii)). Unparasitised *S. formosa* root DW, shoot DW and root : shoot ratio were greater than that of parasitised *S. formosa* at the 33 week harvest.

For each *S. album*: host association the shoot DW increments of *S. album* between week 24 and 33 were compared with the total shoot DW of the host at week 33 (Table 3). *A. ampliceps* shoot DW was significantly greater than that of the other host species at the 33 week harvest but *S. formosa* promoted the greatest *S. album* shoot DW gain between weeks 24 and 33. On this basis *A. trachycarpa* also supported more growth of *S. album* than did *A. ampliceps*. In contrast *E.*

Table 3
Growth of the *Santalum album* and four host species when cultured as single plant pairings under nursery conditions. Values as means±SE. Treatment means followed by the same letter are not significantly different (p>0.05) using Tukey's pairwise t-test. Data are from three replicates

Host species	Shoot dry weight of host (g plant^{-1}) after 33 weeks with the association of *S. album*	Shoot dry weight of *S. album* (g plant^{-1}) after 33 weeks with the association with a host	Shoot dry weight increment of *S. album* (g plant^{-1}) from week 24 to 33 with the association with a host	Shoot dry weight increment of *S. album* per unit dry weight of host shoot (g g^{-1})
Sesbania formosa	59.88 (11.02)c	182.40 (46.98)a	131.07 (44.62)a	2.21 (1.19)
Acacia trachycarpa	30.15 (26.58)c	57.45 (35.21)b	37.97 (54.22)ab	1.77 (3.52)
Acacia ampliceps	277.46 (108.56)a	123.21 (58.37)a	76.60 (62.58)ab	0.35 (0.39)
Eucalyptus camaldulensis	169.53 (48.72)b	17.13 (8.85)b	−2.00 (11.95)b	−0.01 (0.09)
No host	—	35.38 (11.44)b	6.60 (3.47)b	—

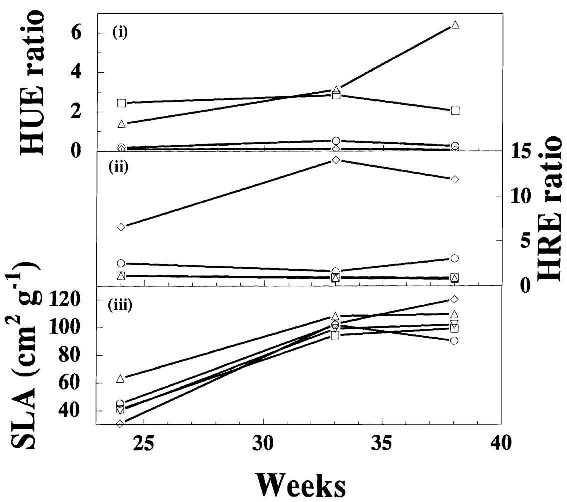

Fig. 8. Changes in *Santalum album* (i) host use efficiency (HUE) (*S. album* shoot dry weight (DW)/host shoot DW), (ii) ratio of the combined host and *S. album* root: *S. album* shoot DW (HRE) and (iii) mean specific leaf area (SLA) while parasitised to (△) *Sesbania formosa*, (○) *Acacia ampliceps*, (□) *A. trachycarpa*, (◇) *Eucalyptus camaldulensis* and (▽) no host. Data are from three replicates. See Table 2 for statistical data.

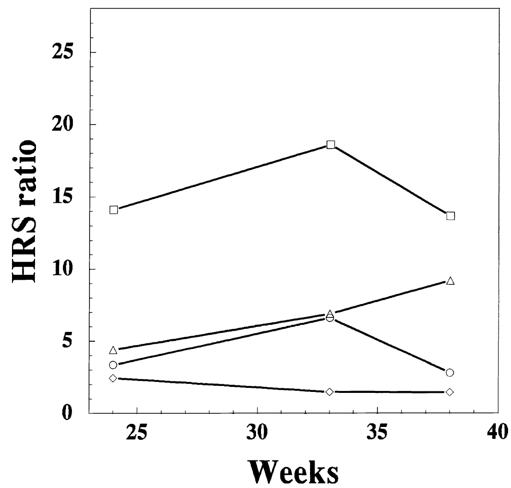

Fig. 9. Changes in the ratio of host shoot DW and *S. album* plant DW : host root DW (HRS) while *S. album* was attached to (△) *Sesbania formosa*, (○) *Acacia ampliceps*, (□) *A. trachycarpa* and (◇) *Eucalyptus camaldulensis*. Data are from three replicates. See Table 2 for statistical data.

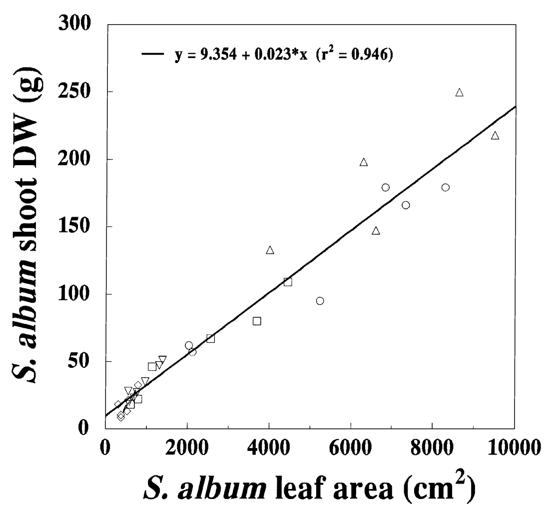

Fig. 10. *Santalum album* shoot DW in relation to *S. album* leaf area for *S. album* attached to (△) *Sesbania formosa*, (○) *Acacia ampliceps*, (□) *A. trachycarpa*, (◇) *Eucalyptus camaldulensis* and (▽) no host. Data are from the 33 week harvest.

camaldulensis was an extremely poor host as *S. album* shoot DW decreased between the two harvests even though *E. camaldulensis* shoot had a high DW. Thus, the HUE (Fig. 8(i)) and the parasites' root : shoot ratios were not correlated to host shoot DW (data not shown).

The combined root biomass of *S. album* and *E. camaldulensis* supported markedly less parasite shoot biomass than the combined root biomass of the other parasite : host associations, as shown by HRE values (Fig. 8(ii)).

There was little difference in *S. album* specific leaf area (SLA) (Fig. 8(iii)). Between the 33 and 38 week harvests the SLA of *S. album* attached to *E. camaldulensis* continued to increase whereas the SLA of *S. album* attached to the other hosts remained constant or decreased.

The total biomass supported by the host root (HRS) was constantly greater for *A. trachycarpa* than that of the other parasite : host associations (Fig. 9). While that for *E. camaldulensis* was constantly lower than that for the leguminous hosts.

S. album shoot DW was positively correlated to plant leaf area (Fig. 10) independent of the host species association.

5. Discussion

5.1. Parasite growth-response to attachment

All three N_2-fixing species were better hosts than the non-N_2-fixing *E. camaldulensis* in promoting parasite growth and on this basis the hypothesis that *S. album* growth is not enhanced when attached to N_2-fixing woody hosts is rejected. This is consistent with Rai (1990) and Taide et al., 1994 who both indicate the N_2-fixing *Casuarina equisetifolia* L. (Casuarinaceae) was a superior *S. album* host from pot culture studies. However these studies did not show conclusively that N_2-fixing species were better *S. album* hosts as several N_2-fixing species, *Albizia lebbeck* (L.) Benth., *Acacia auriculiformis* Cunn. Ex Benth., *Leucaena leucocephala* (Lam.) De Wit (all Mimosaceae) and *Cassia fistula* L. (Caesalpiniaceae) were poorer hosts than several non-N_2-fixing species. A recent pot culture experiment by Tennakoon and Pate (1996) indicated that the N_2-fixing *Acacia littorea* Maslin was a superior host for the root hemi-parasite *O. phyllanthi* than a range of non-N_2-fixing C3 and C4 species. *Phoradendron californicum*, a xylem tapping mistletoe, was recorded with higher growth rates when attached to a N_2-fixing host (Ehleringer et al., 1985).

In terms of promoting overall *S. album* growth, *S. formosa* was the superior N_2-fixing host. However, an important finding from this study was that total *S. album* leaf, stem, shoot and root DW and leaf area continued to increase over time for plants attached to *A. trachycarpa*, whereas growth of all *S. album* plant parts decreased after week 33 for plants attached to the other hosts. This may indicate that *A. trachycarpa* is a more sustainable host. The selection of a suitable intermediate host should thus be performed over an extended period and different species may be optimal depending on the length of time an intermediate host is required.

Growth of unattached *S. album* was consistently greater than the growth of *S. album* when attached to *E. camaldulensis*. This shows that even though *S. album* is an obligate root hemi-parasite its growth may be reduced by attachment to a poor host. There are other reports of poor growth of root hemi-parasites attached to some hosts, such as *O. phyllanthi* attached to *Amaranthus caudatus* L. and *Portulaca oleracea* L. (Tennakoon and Pate, 1996). Tennakoon and Pate (1996) suggest this is a result of the minimal uptake of reduced N due to the large proportion of nitrate in the hosts' xylem sap and as a result heterotrophic C uptake is reduced. Our findings also suggest that *S. album* may be a poor competitor for nutrients in nutrient deficient soils; whereas *E. camaldulensis*, which occurs naturally on low nutrient status soils, appears to be an extremely efficient competitor. It has been proposed that hosts with allelopathic properties retard *S. album* growth (Taide et al., 1994), but there is no direct evidence of this (Fox et al., 1996). Further studies on organic solute transfer from host to *S. album* when grown in association with beneficial and non-beneficial hosts to provide key information on host quality is clearly called for.

The exponential increase in the root : shoot ratio of unattached *S. album* seedlings over time compared to the declining ratio for attached seedlings provides evidence that while in search of a host root system DW is directed to the root system at the expense of the shoot. After attachment, DW partitioning shifts from root to shoot and as a result the root : shoot ratio falls (Radomiljac et al., 1998a).

In an earlier study (Radomiljac et al., 1998a), it was shown that the *S. album* root : shoot ratio declined when *S. album* was attached to larger *Alternanthera* pot hosts and it was hypothesised that *S. album* used the host root system as an extension of its true root system to support a large shoot biomass. In this study no relationship exists between *S. album* root : shoot ratio and the DW of various host species suggesting that the relationship only applies when *S. album* is attached to plants of different sizes of the same host species.

The host root system may be viewed either as supporting the parasite's total biomass coupled with supporting its own shoot or as an extension of the parasite's own root system. The HRE value for *S. album* attached to *E. camaldulensis* was far higher than that for *S. album* attached to N_2-fixing hosts, which were comparatively uniform over time. This suggests that the combined *S. album* and *E. camaldulensis* root system performed poorly, relative to the parasite : N_2-fixing host associations, by only supporting a small *S. album* shoot. Conversely, the HRS value for *S. album* attached to *E. camaldulensis* was consistently lower than the parasite : N_2-fixing host associations. An interesting observation is that while *A. trachycarpa* had the smallest root system its HRS value was significantly greater than the other parasite : host associations. This suggests there is considerable variation between N_2-fixing species in ability to support the legume shoot biomass coupled with supporting the whole *S. album* biomass.

S. album SLA was similar for *S. album* attached to all hosts however plant leaf area was strongly related to *S. album* shoot DW regardless of host species. This is consistent with non-parasitic plants where a linear relationship exists between tree growth and plant leaf area independent of irrigation and fertilisation (Nambiar, 1990; Stoneman and Dell, 1993). Stoneman and Dell (1993) indicated that irrigation and fertilisation increase leaf area, which increases radiation interception and leads to an increase in growth. N_2-fixing hosts increased *S. album* leaf area, which was positively correlated to increased parasite growth. *S. album* leaf area index may be a useful predictor of plantation productivity where host quality influences growth.

5.2. Host growth-response to parasitism

S. album usually develops into a large tree in its native and naturalised habitats of eastern Indonesia (Harisetijono and Suriamihardja, 1993) and southern India (Srinivasan et al., 1992). While most root hemiparasites such as *Rhinanthus serotinus* Schonh. (Klaren and Jansen, 1978), *O. phyllanthi* (Pate et al., 1990) and *Striga hermonthica* (Del.) Benth. (Musselman, 1980) remain smaller than their hosts, *S. album*, other *Santalum* species and *Nutysia floribunda* (Labill.) R. Br. (Hocking, 1980) are often larger than their hosts.

In this study, the decline in *S. formosa* biomass (96% decrease in leaf area) is evidence of the substantial drain by *S. album* of the resources of a good host species. This has also been shown for other species (Graves et al., 1990; Graves, 1995; Tennakoon and Pate, 1996). *S. album* must therefore be classified as a debilitating hemi-parasite. The deleterious effect on *S. formosa* growth may be attributed to *S. album*'s large size, high growth and metabolic rate and high heterotrophic dependency (Graves, 1995). *S. album* may have reduced the growth of *S. formosa* by acting as an additional sink for *S. formosa* carbon and reducing its capacity to fix carbon (Tuohy et al., 1987; Graves et al., 1990). However, this is not consistent with the growth patterns of *A. trachycarpa* and *A. ampliceps* which continued to grow under parasitism. Graves (1995) hypothesises that host size and vigour influences the level of damage by the parasite. Even though *A. trachycarpa* and *S. formosa* possessed similar levels of sink resistance (biomass) the greater size of *S. album* attached to *S. formosa* compared to that attached to *A. trachycarpa* suggests more host assimilates were removed from *S. formosa*, resulting in greater host decline.

6. Conclusion

This pot study showed that association with N_2-fixing woody hosts increased early *S. album* growth. *S. formosa* was the superior N_2-fixing host as it promoted greatest *S. album* growth, but *A. trachycarpa* may sustain *S. album* growth for a longer period. Growth of *S. album* without a host was consistently greater than the growth of *S. album* when grown with *E. camaldulensis*, indicating that poor hosts may suppress parasite growth. The large differences in *S. album* growth when grown with different host species in this study highlights the importance of identifying suitable intermediate hosts to promote early *S. album* plantation growth.

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