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Heterotrophic carbon gain and mineral nutrition of the root hemi-parasite *Santalum album* L. in pot culture with different hosts.

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Summary

This paper examines heterotrophic gain of carbon and mineral composition of *Santalum album* partnered singly in pot culture with three beneficial woody N₂-fixing hosts and a non-beneficial eucalypt host. Based on dry matter gains of the parasite at 33 weeks, *Sesbania formosa* proved the best host followed by *Acacia ampliceps* and *A. trachycarpa* while no improvement in growth was seen with *Eucalyptus camaldulensis* as a host in comparison with *Santalum* grown without a host. Numbers of haustoria formed by *Santalum* on roots of different hosts were poorly correlated with host quality. A small proportion of haustoria on legume hosts were attached to root nodules. *Santalum* partnered with any host or grown alone exhibited self-parasitism where haustoria attached to its own root system.

Based on net C and N gains of *Santalum* and the C : N ratios of xylem solutes of *Santalum*, the heterotrophic gains of C from xylem of the three beneficial legume hosts over a nine week period were equivalent to 57.9% of total carbon (35.9 g C plant⁻¹) on *A. ampliceps*, 45.5% (12.7 g C plant⁻¹) on *A. trachycarpa* and 34.6% (29.9 g C plant⁻¹) on *S. formosa*.

Assays of leaf, stem, bark and root tissue of *Santalum* and its hosts and net increases in mineral contents of *Santalum* over the first nine weeks of the study showed that parasitism on beneficial hosts increased the mineral contents of the parasite, with evidence of net gains in certain elements (e.g. Ca, K, P, Na) being greatest when associated with hosts richest in the corresponding element. Foliage of *Santalum* was extraordinarily rich in Na and in some cases also in P and N in comparison with associated hosts. Net losses or only small gains of P, K, Ca and Na over the study interval in *Santalum* grown alone or associated with the eucalypt indicated poor ability for nutrient uptake through its own root system.

Regression analysis showed incremental gains of N, C and Na, leaf area, content of K, N and Na in foliage of the parasite and root : shoot ratio to be excellent predictors of growth benefit from different hosts. Examples of stepwise regression analysis are provided indicating how such data might be employed for monitoring growth and host benefit under future plantation cultures of the parasite.

Introduction

Santalum album L., commonly known as Indian sandalwood or chandana, is commercially and culturally a most important root hemi-parasite, subject to considerable exploitation since at least 1000 BC (Srinivasan *et al.* 1992). Strong interest now exists in cultivating the species in mixed species plantations throughout the tropics (Hamilton and Conrad 1990; McKinnell 1993; Havel and McKinnell 1993; Gjerum *et al.* 1995; Radomiljac *et al.* 1998a). There are considerable uncertainties regarding the best culture and management prac-

tices in relation to the best host species, and how to achieve the highest volume and quality of sandalwood in a particular set of environmental circumstances.

Our current projects, aimed at defining the best protocols for growth of *S. album* under irrigation culture in the Ord River region of North West Australia, have utilised a native herbaceous perennial, *Alternanthera nana* R. Br., as a host during pot culture with seedlings of the parasite, followed by use of various fast growing but relatively short lived species as 'intermediate hosts' once plants are transferred to the field. Ultimately it is hoped that the *Santalum* will parasitise long-lived valuable timber trees such as the leguminous *Dalbergia* (Papilionoideae tribe Dalbergaeae) until it reaches harvestable size. While the system has yet to be tested in the field beyond the 4 year stage, it is already apparent in both pot and plantation culture that in contrast to a eucalypt host, N₂-fixing hosts promote much greater dry weight gain, leaf N concentrations, photosynthetic rates and water use efficiencies in the parasite, but lower root : shoot ratio and C : N ratio of organic solutes in the xylem sap of the parasite (Radomiljac *et al.* 1998b, c, d). These findings concur with the conclusions from a number of other studies that N₂-fixing hosts are more effective than non N₂-fixing hosts in promoting growth of angiosperm parasites, presumably or demonstrably as a result of greater enrichment of transport streams with N in the N₂-fixing species (Schulze and Ehleringer 1984; Rai 1990; Seel and Press 1993; Seel *et al.* 1993; Chechin and Press 1993; Taide *et al.* 1994; Tennakoon and Pate 1996b).

In this paper we build further upon our earlier pot culture studies on *Santalum* (Radomiljac *et al.* 1998b, c, d) to determine the heterotrophic inputs of carbon to *Santalum* through uptake of xylem solutes from different hosts, and also how the mineral nutrition of *Santalum* is modified through attachment to different hosts. Then, using this information together with earlier measured attributes of performance on different hosts, we evaluate the relative usefulness of different growth and compositional features of parasite and host in ranking growth benefit to the parasite from different hosts under a specific set of cultured conditions.

Materials and methods

The effect of beneficial and non-beneficial woody hosts on the heterotrophic carbon gain and mineral composition of pot cultured *S. album* seedlings was studied in a nursery near Kununurra (lat 15°46' S. long 128°44' E), Western Australia. The four intermediate hosts selected for matching with *Santalum* were the N₂-fixing *Sesbania formosa* (F. Muell.) N. Burb., *Acacia trachycarpa* E. Pritzel, *A. ampliceps* Maslin, and the non N₂-fixing *Eucalyptus camaldulensis* Dehnh. *Santalum* grown singly without a host comprised a control.

In July 1996, 40 uniform 6-month old *S. album* seedlings

(mean height \pm std error; 40.5 ± 2.98 cm and diameter; at 2 cm, 3.9 ± 0.58 mm) were selected. Each had been cultured singly in 1.4 litre pots with the native herbaceous *Alternanthera nana* as an initial pot host. The *Alternanthera* was then cut to soil level and the *Santalum* transplanted to 25 litre pots of coarse river sand : peat : perlite at 3 : 2 : 2. A single seedling of one of the intermediate hosts previously propagated in 0.3 litre pots was introduced into each pot at about 150 mm from the single *Santalum* seedling. The legume hosts were inoculated with appropriate *Bradyrhizobium* (see Radomiljac *et al.* 1998b). Remaining host seedlings formed a series of control unparasitised plants. A 10 g dressing of 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 0.4%, Mn 0.06%, Mo 0.02% and Zn 0.015%) was applied to the surface of each pot. Pots were placed on mesh benches 10 cm above ground to avoid possible intrusion of roots from one pot to neighbouring treatments. Four weeks following transplanting as much as possible of the remaining *Alternanthera* was removed and all host : parasite pairings cultured in the nursery for a further 8 months in full sun with overhead watering twice daily, for approximately 15 minutes, to near field capacity. Using these culture conditions it was hoped that cultures would become moderately nutrient deficient, thereby accentuating the dependence of the parasite on host xylem solutes for its growth.

Five pots per treatment, as single pot plots, were randomised within each of eight replicates. The position of the replicate and pots within each replicate were rearranged in random fashion twice during the course of the study.

At each of two harvest times (12 December 1996 and 17 February 1997) three pots were selected for harvesting from each treatment. Harvested plants were chosen carefully, with one of the selected plants of *Santalum* approximately equal to the current mean stem diameter (2 cm above ground level) of all plants of that treatment, the second plant one Standard Deviation (SD) unit greater, and the third one SD less than this diameter. This ensured that each harvest was representative of all the plants in each treatment. *Santalum* and host plants were harvested by cutting the stem at soil level and the shoots were partitioned into stem, bark and leaf material. Pots with intermingled root systems of *Santalum* and host root systems still intact were then cut horizontally into three layers, 0–8 cm, 8–16 cm and 16–24 cm from top to bottom of the pot. The rooting medium was then carefully vacuumed away from the intermingled roots, taking care not to lose fine root material in the process. This procedure was preferred to washing and sieving as roots of host and parasite tend to remain in contact with each other, thus facilitating counting of haustoria and determining whether haustoria were (a) connected to host root xylem tissue, (b) connected to nodules in the case of leguminous hosts, or (c) connected to other *Santalum* roots (auto-parasitic).

The morphology and anatomy of haustoria of *Santalum* were studied in partnership with three of the legume hosts, using mature haustoria attached either to host roots or to symbiotically active nodules. Haustoria were fixed in 2.5% glutaraldehyde in 0.025M phosphate buffer (pH 7.0). After ethanol dehydration and embedding in wax, sections were cut at 10 mm through the haustoria – nodule plane and stained in 1% aqueous toluidine blue. Alternatively, specimens were dehydrated in acetone, embedded in Spurr's resin, cut at 1 mm and stained in 1% methylene blue and 1% azure II in 1% borax.

Harvested leaf, stem, bark and root material of parasite and hosts were oven dried at 80°C for 48 hours and finely milled for chemical analysis. Total N in dry matter of plant samples was determined by the Kjeldahl digestion method (McKenzie and Wallace 1954), and K, Ca, Mg, Na, Fe, Cu, Mn and Zn assayed using a nitric/perchloric acid digestion procedure followed by atomic absorption spectrophotometry of appropriately diluted digests (see Pate *et al.* 1991). Total P was estimated separately on the digests using the colourimetric molybdenum blue method (Kitson and Mellon 1944).

Data for haustorial frequencies or mineral nutrient contents in plant dry matter were analysed using ANOVA and Tukey's pairwise t-test. All analyses were performed using SYSTAT® statistical software (Systat 1992). Linear regression and stepwise multiple regression procedures for predicting *Santalum* dry weight were performed using the regression procedure of SYSTAT®.

The formula used for estimating the heterotrophic gain of carbon (H) by *Santalum* when grown as single pairwise plantings with a particular N₂-fixing host was as follows :

$$H = C:N_{xs} * (TN^1 - TN^2)$$

Where C:N_{xs} is the C : N ratio of the total organic solutes of xylem sap of *Santalum* grown with N₂-fixing host, TN¹ is the incremental gain of N of *Santalum* when grown on the same host and TN² is the incremental gain of N of *Santalum* cultured without a host. The following assumptions are made : (a) N uptake by the parasite from the potting medium was the same when growing with a host and when grown alone, (b) all N in parasitic *Santalum* additional to that accumulated when grown alone represents fixed or medium derived N abstracted by the parasite from host xylem (Press *et al.* 1987; Tennakoon and Pate 1996b) and (c) organic solutes recovered from xylem sap of *Santalum* were representative of the proportional amounts of C and N currently being gained from the host (Tennakoon and Pate 1996b). The analysis used C and N contents of dry matter and C : N ratios obtained earlier from analysis of xylem solutes (Radomiljac *et al.* 1998c) of the same *Santalum* cultures used in this study.

Results

Haustrorial numbers and sitings of attachments

The number of mature haustoria attached to host roots and presumably penetrating to xylem tissue varied considerably with the host species which was being parasitised (Figure 1), but a very strong correlative relationship ($r^2 = 0.99$, $p = 0.066$, $n = 12$) existed between haustorial number on a host and root dry weight of that host. However, somewhat surprisingly, a poor and non-significant correlation was found between haustorial number and the extent of benefit to *Santalum*, as gauged by its shoot or root DW at the time of harvest. This finding contrasts with the results of Tennakoon *et al.* (1997b) who reported a strong positive relationship of this nature for *Oxalaphyllanthi* (Labill.) R. Br. pot cultured with single hosts. Figure 1 shows a relatively small proportion of haustoria were attached to nodules on leguminous hosts compared with the total number on the same hosts. However there was a strong positive, although non-significant, relationship between the number of haustoria connected to nodules and *Santalum* shoot DW ($r^2 = 0.87$, $p = 0.238$, $n = 9$) and a significant positive correlation to *Santalum* root DW ($r^2 = 0.99$, $p = 0.031$, $n = 9$). The level of autoparasitism, involving haustorial connections of *Santalum* onto its own roots, was appreciable in all associations, but never exceeded more than 27% of the total

number of haustorial connections recovered from a pot. Self-parasitism was also prevalent on plants of *Santalum* grown without a host (Figure 2b).

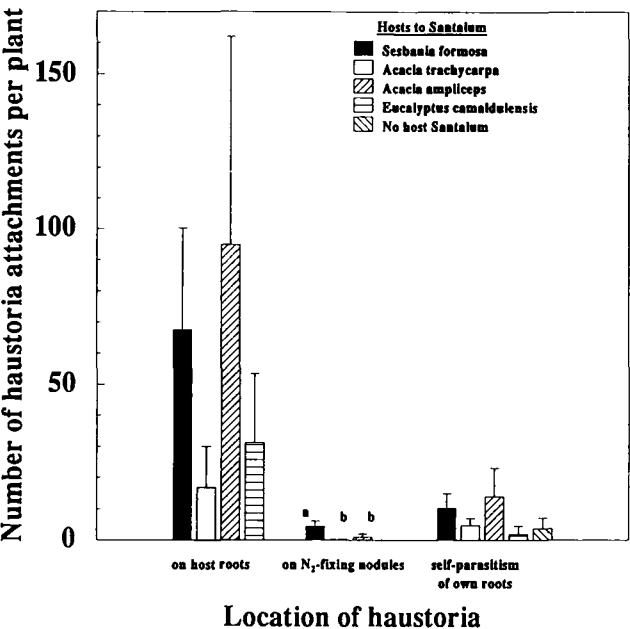


Figure 1. Number of haustorial attachments made by *Santalum album* on host roots, N₂-fixing nodules and on its own roots when cultured as single plant pairings with four host species or without a host at second harvest at 33 weeks. Values are means with standard error bars shown. Treatment means of haustoria attachments on N₂-fixing nodules followed by the same letter are not significantly different (*p* > 0.05) using Tukey's pairwise t-test. Treatment means for haustoria on roots of different hosts were not significantly different, neither were data on haustorial formation by the parasite on its own roots. Data are from 3 replicates.

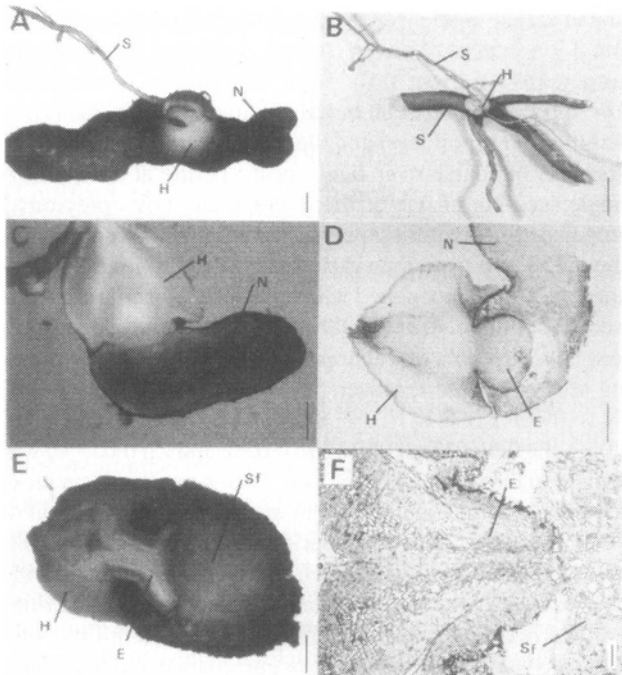


Figure 2. *Santalum album* haustoria on (A) *Acacia trachycarpa* nodule, bar = 1mm; (B) *Santalum* roots (self parasitism), bar = 1 cm; (C) *A. trachycarpa* nodule. An immature haustorium on a functional nodule, section through fresh material, bar = 1mm; (D) *A. trachycarpa* nodule, bacterioids in this nodule have degenerated and there is a zone of tissue disintegration at the face of the endophyte, section wax embedded, cut at 10mm and stained in toluidine blue, bar = 1mm; (E) *Sesbania formosa* root, bar = 1mm; (F) *S. formosa* root in TS, section resin embedded, cut at 1mm and stained in methylene blue and azure II, bar = 0.1mm. S, *S. album* root. H, *S. album* haustorium. N, *A. trachycarpa* root nodule. E, endophyte of haustorium. Sf, *S. formosa* root.

Table 1 : Total carbon and nitrogen contents and concentration of shoots of *Santalum* and associated host species, cultured as single plant pairings. Corresponding data for non-parasitised hosts are included for each host species. Data are means \pm std errors. Data for *Santalum* and parasitised hosts are from 3 replicates from the harvest at week 33 of parasite : host association. Data for unparasitised hosts are from 1 replicate.

| | Parasite : Host association | | | | |
|--|---------------------------------------|---|---|---|-----------------------------|
| | <i>Santalum:</i> <i>S. formosa</i> | <i>Santalum:</i> <i>A. ampliceps</i> | <i>Santalum:</i> <i>A. trachycarpa</i> | <i>Santalum:</i> <i>E. camaldulensis</i> | No host: <i>Santalum</i> |
| <i>Santalum</i> shoot DW (g) ^a | 182 \pm 46.9 | 123 \pm 58.4 | 57.5 \pm 35.2 | 17.1 \pm 8.8 | 35.6 \pm 11.4 |
| Parasitised host shoot DW (g) ^a | 59.9 \pm 11.0 | 277 \pm 108 | 30.2 \pm 26.6 | 169 \pm 48.7 | - |
| Non-parasitised host shoot DW (g) ^a | 394 | ND ^c | 100 | 239 | - |
| C concentration of <i>Santalum</i> shoot (%) ^b | 47.6 \pm 0.3 | 48.5 \pm 1.0 | 50.0 \pm 0.7 | 43.7 \pm 0.6 | 47.7 \pm 1.24 |
| C concentration of parasitised host shoot (%) ^b | 49.6 \pm 0.5 | 45.3 \pm 0.8 | 49.0 \pm 1.3 | 46.7 \pm 0.4 | - |
| C concentration of non-parasitised host shoot (%) ^b | 46.9 | ND | 43.4 | 47.0 | - |
| Total C of <i>Santalum</i> shoot DW (g) | 86.8 | 59.8 | 28.7 | 7.49 | 17.0 |
| Total C parasitised host shoot DW (g) | 29.7 | 125 | 14.8 | 79.2 | - |
| Total C of non-parasitised host shoot DW (g) | 184 | ND | 43.7 | 112 | - |
| N concentration of <i>Santalum</i> shoot (%) ^b | 1.41 \pm 0.2 | 1.22 \pm 0.1 | 1.20 \pm 0.1 | 0.59 \pm 0.04 | 0.55 \pm 0.01 |
| N concentration of parasitised host shoot (%) ^b | 0.79 \pm 0.1 | 1.04 \pm 0.04 | 1.35 \pm 0.1 | 0.32 \pm 0.02 | - |
| N concentration of non-parasitised host shoot (%) ^b | 1.01 | ND | 1.31 | 0.32 | - |
| Total N of <i>Santalum</i> shoot DW (g) | 2.57 | 1.50 | 0.69 | 0.10 | 0.19 |
| Total N parasitised host shoot DW (g) | 0.47 | 2.88 | 0.41 | 0.54 | - |
| Total N of non-parasitised host shoot DW (g) | 3.98 | ND | 1.32 | 1.29 | - |

^a Data from Radomiljac *et al.* (1998b).
^b Data from Radomiljac *et al.* (1998c).
^c No data.

Endophytes of haustoria that penetrated nodules were examined for all three legume hosts. The point of entry of the endophyte was apparently random in relation to the gross morphology of the nodule and in all cases failed to connect to the peripheral vasculature of the nodule (Figures 2a and c). Endophytes within nodules were bulbous, in comparison with the typical flattened endophytes observed against the xylem of host roots (Figure 2d and e). There was usually a marked gap between the absorbing face of the endophyte and bacterial tissue of the nodule. Disintegration of bacterioids and collapse of nodule cells was evident in older nodules (Figure 2d). There appeared to be less development of vascular tissue in the endophytes of haustoria on nodules than in those attached to roots (Figures 2d and f).

C and N content of *Santalum* and parasitised and unparasitised hosts

C and N concentration and contents of *Santalum* shoots grown in association with *S. formosa* were much greater than those of any other association. *Santalum* grown in association with *E. camaldulensis* showed considerably less C and N content than in any other association and less also than in *Santalum* grown without a host. As would be expected from the drain made on host resources by the presence of the parasite, growth and associated C and N contents of unparasitised hosts were consistently much greater than in those that were parasitised, the largest differences being recorded for *S. formosa* (Table 1).

Estimates of proportional heterotrophic gain (H) of carbon by *Santalum* on N₂-fixing hosts

Santalum grown with *S. formosa* had the greatest increment of C and N over a nine week period, whereas C and N increment of *Santalum* grown without a host was considerably lower than when grown with N₂-fixing hosts (Table 2). Estimates of H based on calculations from the C : N ratios of total organic solutes in xylem sap and N increments of parasitised *Santalum* over those of *Santalum* alone showed C gain from *S. formosa* (29.9 g C plant⁻¹), followed by *A. ampliceps* (about 35.9 g C plant⁻¹) and *A. trachycarpa* (12.7 g C plant⁻¹). The C gains are equivalent to 34.6%, 57.9% and 45.5% of net C increments in *Santalum*.

Mineral nutrient distribution of parasite and host

N, P, K, Ca, Mg and Na contents in dry matter for various plant parts of all *Santalum* : host associations harvested at 33 weeks are shown in Figure 3a-h (Data for Fe, Mn, Zn and Cu are not shown). Mineral nutrient contents of *Santalum* plant parts when grown in partnership with *E. camaldulensis* differed little from those of *Santalum* grown without a host, consistent with little or no dry matter benefit to *Santalum* resulting from association with this host (Table 1). By contrast *Santalum* attached to any of the leguminous hosts showed contents of N and K in plant parts which were significantly greater than in corresponding parts of *Santalum* growing without a host. The reverse applied to P, Na and Mg. As expected, levels of all nutrients were higher in bark than in stem tissue as recorded earlier for a mistletoe by Tennakoon and Pate (1996a).

Table 2 : Proportional heterotrophic gain of carbon by the root hemi-parasite *Santalum* calculated from the C : N ratio of total organic solutes in *Santalum* xylem sap and the difference between the incremental gain of N of *Santalum* when grown with or without a N₂-fixing host.

| | Parasite : Host association | | | |
|--|--|--|--|-----------------------------|
| | <i>Santalum</i> : <i>S. formosa</i> | <i>Santalum</i> : <i>A. ampliceps</i> | <i>Santalum</i> : <i>A. trachycarpa</i> | No host: <i>Santalum</i> |
| C : N ratio of total organic solutes from <i>Santalum</i> xylem sap ^a | 18.0 | 28.3 | 21.5 | 102 |
| <i>Santalum</i> DW 24 weeks after parasite : host association (g plant ⁻¹) ^b | 110 | 52.9 | 50.8 | 35.7 |
| <i>Santalum</i> DW 33 weeks after parasite : host association (g plant ⁻¹) ^b | 292 | 180 | 106 | 60.9 |
| <i>Santalum</i> DW increment over a 9 week period (g plant ⁻¹) ^b | 181 | 127 | 55.7 | 25.2 |
| Total C of <i>Santalum</i> at 24 weeks (g plant ⁻¹) ^c | 52.4 | 25.7 | 25.3 | 17.0 |
| Total N of <i>Santalum</i> at 24 weeks (g plant ⁻¹) ^c | 1.55 | 0.64 | 0.61 | 0.19 |
| Total C of <i>Santalum</i> at 33 weeks (g plant ⁻¹) ^c | 138 | 87.6 | 53.1 | 29.0 |
| Total N of <i>Santalum</i> at 33 weeks (g plant ⁻¹) ^c | 4.11 | 2.20 | 1.27 | 0.33 |
| DC of <i>Santalum</i> dry matter from 24 to 33 weeks (g plant ⁻¹) | 86.6 | 62.0 | 27.8 | 12.0 |
| DN of <i>Santalum</i> dry matter from 24 to 33 weeks (g plant ⁻¹) | 2.56 | 1.6 | 0.66 | 0.14 |
| C : N ratio of <i>Santalum</i> dry matter increment | 33.7 | 39.8 | 41.6 | 86.7 |
| Difference between incremental N of <i>Santalum</i> when grown with N ₂ -fixing hosts and without a host over a 9 week period (g plant ⁻¹) | 1.66 | 1.27 | 0.59 | - |
| Heterotrophic gain of C of <i>Santalum</i> from host based on C : N ratio of total organic solutes in <i>Santalum</i> xylem sap and incremental gain of N of <i>Santalum</i> when grown with N ₂ -fixing hosts and without a host over a 9 week period (g plant ⁻¹) | 29.9 | 35.9 | 12.7 | - |
| Values for H as % of total C gain of parasite from 24 to 33 weeks | 34.6 | 57.9 | 45.5 | - |

^a Data from Radomiljac *et al.* (1998c) ^b Data from Radomiljac *et al.* (1998b) ^c Data from Table 1

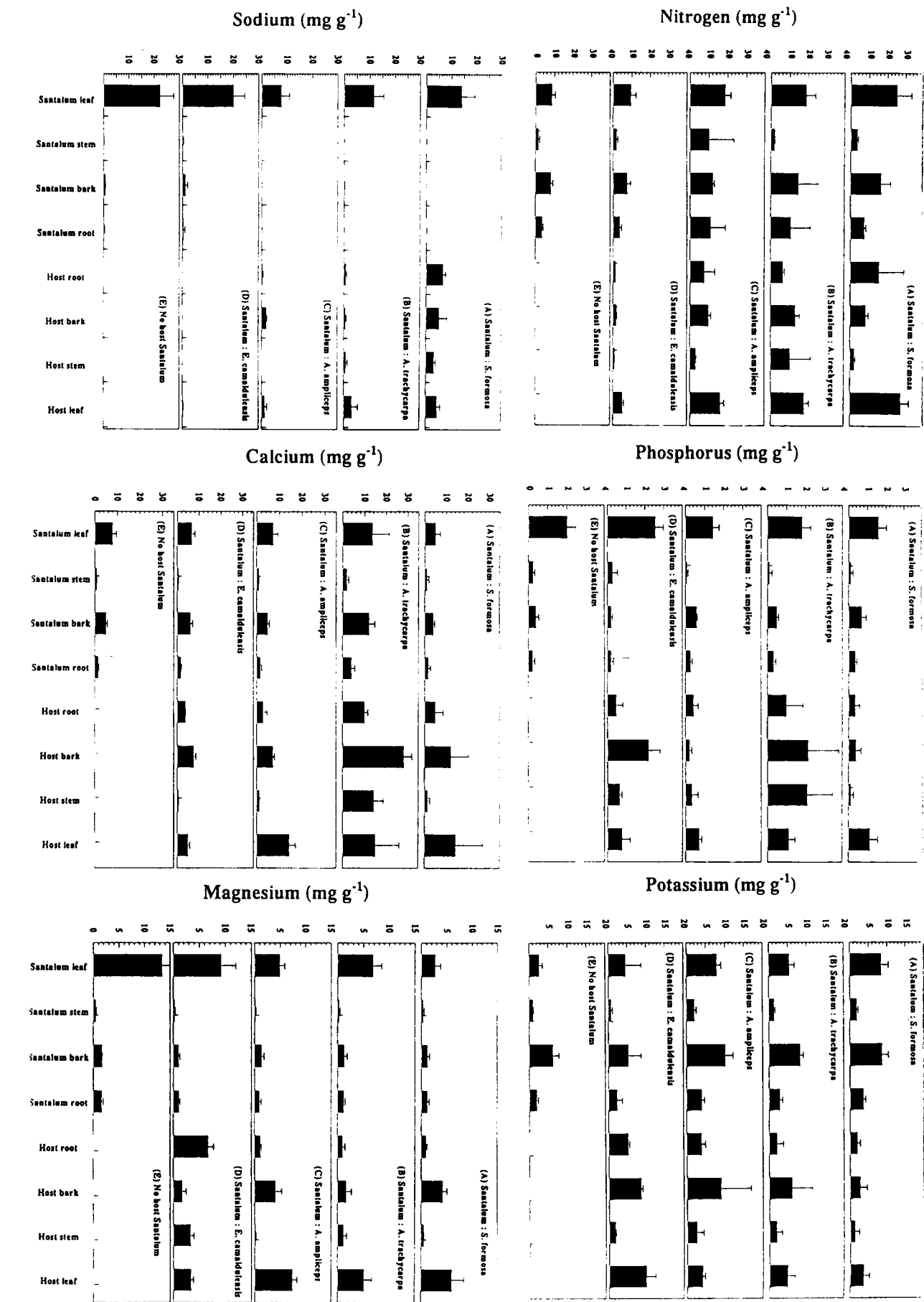


Figure 3. The contents of nitrogen (a), phosphorus (b), potassium (c), sodium (d), calcium (e) and magnesium (f) of leaf, stem, bark and root tissue in *Santalum* and its hosts (A) *Sesbania formosa*, (B) *Acacia trachycarpa*, (C) *A. ampliceps* or (D) *Eucalyptus camaldulensis* or when grown without a host (E). Data are from 3 replicates from the second harvest at week 33 of parasite : host association. See Table 3 for statistical data.

Analysis of all mineral nutrient data for *Santalum* indicated that contents of N, P, K, Ca, Mg, Mn, Na and Fe in leaves, of K and Zn in stem wood and K and Ca in roots were all significantly affected by the host to which *Santalum* was attached (Table 3).

Increments in dry weight, N, P, K, Ca and Na of *Santalum* on different hosts

Changes in total contents of N, P, K, Ca and Na in *Santalum* from week 24 to week 33 indicated that relative to dry weight increment, there was a disproportionately greater increase in N when the parasite was grown on any legume host, but it was greatest with *S. formosa*. There was also a greater increase in Na when grown on *S. formosa*, in P and K when on *A. ampliceps* and Ca when on *A. trachycarpa* and *S. formosa* (Figure 4a-f). Net decreases or only slight increases in N, P, K, Ca and Na content in *Santalum* grown on *E. camaldulensis* or without a host were generally indicative of poor growth of such cultures in the latter part of the growth period. Strong positive correlations were demonstrated between *Santalum* dry weight increment and total N ($r^2 = 0.97$, $p = 0.002$, $n = 15$) and Na increment ($r^2 = 0.88$, $p = 0.019$, $n = 15$).

Discussion

Despite extensive studies on the carbon and water economies and mineral nutrition of root hemiparasitic plants and their hosts, in both pot culture and native habitat (Hocking 1980; Lamont and Southall 1982; Glatzel 1983; Schulze and Ehleringer 1984; Struthers *et al.* 1986; Pate *et al.* 1991; Seel and Press 1993; Tennakoon and Pate 1996a; Veenendaal *et al.* 1996; review by Pate 1995), limited definitive information exists on mechanisms and extents of benefit in terms of heterotrophic gains of carbon and acquisition of specific mineral elements from hosts. Using *Santalum* partnered singly with leguminous and a non-leguminous host, an attempt is made in this paper to quantify benefits and thus rank hosts in terms of suitability as donors of organic and inorganic solutes to the parasite.

Our study confirms for *S. album* the general conclusion that

xylem-tapping root hemi-parasites grow best when associated with N_2 -fixing legume hosts, apparently as a result of greater N concentrations in the xylem of legumes compared to non legumes (Subbarao *et al.* 1990; Cechin and Press 1993; Seel and Press 1993; Tennakoon and Pate 1996b; Tennakoon *et al.* 1997a, b, c; Radomiljac *et al.* 1998b, c). Since the pot culture conditions in this study provided only a small initial dressing of N in the form of slow release fertiliser the unsurpassed benefit from nodulated legume hosts to *Santalum* comes from the abstraction of fixed N. Conversely, *Santalum* partnered with *E. camaldulensis* had to compete with its host for the fertiliser N applied and not surprisingly grew extremely poorly compared to those plants on legume hosts and amassed only half the dry weight of plants grown without hosts (Table 1).

As further evidence of competition, as opposed to benefit to *Santalum*, the root biomass of the eucalypt was much greater than that of other hosts while the root mass of the *Santalum* was less than in any other treatment. At the other extreme, *A. trachycarpa*, the host with the smallest root biomass, promoted growth of a root system in the associated *Santalum* four times larger, in terms of mass, than when parasitising *E. camaldulensis* (Radomiljac *et al.* 1998b).

Somewhat surprisingly this study showed a very poor relationship between haustorial number and resulting growth benefit of *Santalum*. For example, *Santalum* parasitising *A. trachycarpa* established only half the number of haustoria as the *Santalum* : *E. camaldulensis* association, yet benefit from the former host was very much greater. Of course, counts or even weights of haustoria offer no direct evidence of benefit and without sectioning and proof of uptake from host xylem, their efficacy remains unproven. Indeed, Santalacean root hemi-parasites can attach to inanimate objects such as small stones, decaying plant material, surfaces of pots and particularly to slow-release fertilizer pellets (A. M. Radomiljac unpublished observations; Hocking and Fineran 1983; Pate *et al.* 1990b). In the present study we report also on direct parasitism of the nodules of legume hosts, as described for *Olex phyllanthi* haustoria on nodules of *Acacia littorea* Maslin (Tennakoon *et al.* 1997b). In both cases haustoria penetrat-

Table 3 : The effects of an intermediate host species on mineral distribution in *Santalum* and the host, 33 weeks after commencement of parasite : host association as single plant pairings.

| Dependent variable | Mineral | | | | | | | | | | | |
|--------------------|--------------------|-------|-------|-------|-------|-----------------|-------|-------|-------|-------|-------------|--------------|
| | N | P | K | Ca | Mg | Zn | Cu | Mn | Na | Fe | N : P ratio | K : Na ratio |
| <i>Santalum</i> | | | | | | | | | | | | |
| Leaf | 0.000 ¹ | 0.001 | 0.001 | 0.008 | 0.000 | ns ² | ns | 0.000 | 0.000 | 0.001 | 0.000 | 0.000 |
| Stem | ns | ns | 0.001 | ns | ns | 0.002 | ns | ns | ns | ns | ns | 0.004 |
| Bark | ns | 0.005 | ns | 0.000 | ns | ns | ns | 0.029 | ns | ns | ns | ns |
| Root | ns | ns | 0.041 | 0.026 | ns | ns | ns | ns | ns | ns | ns | ns |
| <i>Host</i> | | | | | | | | | | | | |
| Leaf | 0.000 | ns | 0.000 | ns | 0.001 | ns | 0.000 | 0.000 | 0.000 | ns | 0.000 | 0.000 |
| Stem | ns | 0.029 | ns | 0.000 | 0.038 | 0.002 | ns | 0.001 | 0.000 | ns | ns | 0.000 |
| Bark | 0.000 | 0.036 | ns | 0.001 | 0.012 | 0.001 | 0.001 | 0.004 | 0.010 | 0.001 | ns | 0.000 |
| Root | ns | ns | 0.048 | 0.027 | 0.003 | ns | ns | ns | 0.000 | 0.009 | ns | 0.037 |

¹, Numbers are the probability of accepting the null hypothesis of no difference in treatment means.

², Treatment means are not significantly (ns) different from each other ($p > 0.05$).

ing nodules represented very small proportions of the total contacts made with a host and quickly resulted in degeneration of nodule bacterial tissue and therefore, presumably, cessation of fixation in that nodule. On these grounds attachment to nodules is likely to yield minimal benefit compared with longer term and more prolific contacts between haustoria and root xylem.

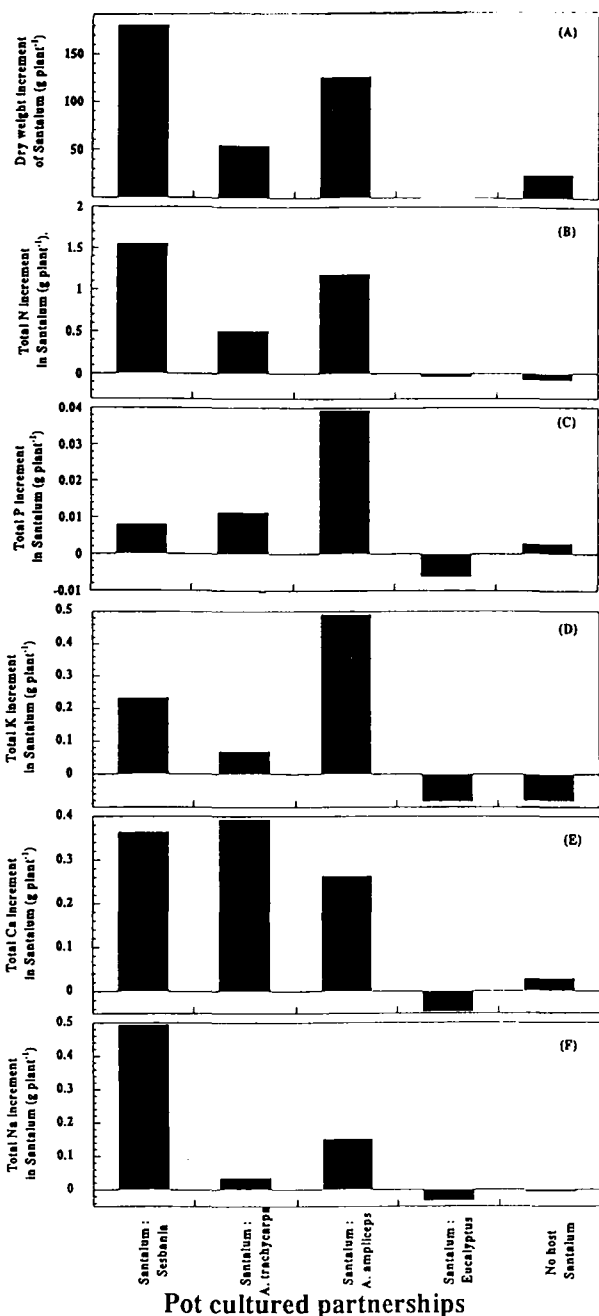


Figure 4. Increment in the root hemi-parasite *Santalum* (A) dry weight, (B) nitrogen, (C) phosphorous, (D) potassium, (E) calcium and (F) sodium over a nine week period of effective attachment (week 24 to 33 of association) when partnered singly with *Sesbania formosa*, *Acacia trachycarpa*, *A. amplexica* or *Eucalyptus camaldulensis* or when grown without a host.

It has been long accepted for plants generally that N deficiency results in abnormally greater partitioning of assimilates to the root as opposed to shoots. This results in higher root : shoot ratios and may be viewed as a mechanism for exploiting greater possible volumes of soil towards improvement of N uptake (Linder and Rook 1984; Nambiar 1990;

Stoneman and Dell 1993). In a similar manner, young, as yet unattached seedlings of *Santalum* show preferential partitioning of biomass to their root system (Radomiljac *et al.* 1998e), but following attachment to a beneficial host, biomass partitioning shifts progressively in favour of the shoot. The high N : P ratio of *Santalum* foliage when grown on legume hosts (10.5 – 17.2) compared with that when grown on *E. camaldulensis* (3.8), or without a host (4.4), provides confirmation of the extent to which a legume host alleviates N-deficiency of the parasite. However, N : P ratios for *S. album* recorded on N₂-fixing hosts in this study were 2 to 3 times lower than those reported for *S. spicatum* (R. Br.) A. DC. when attached to *Acacia acuminatum* Benth. in native habitat (Struthers *et al.* 1986). Presumably P limitation applied to the ecosystem where *S. spicatum* was growing, whereas the slow release fertiliser used in this study was likely to have provided non-limiting amounts of P but not of N.

In this paper we employ a novel technique for estimating heterotrophic gains (H) of C by *Santalum*, by matching the C : N ratio of the organic solutes of its xylem sap when grown on a N₂-fixing host, with the difference between the incremental gain of N of *Santalum* grown with the same host, and that when grown without a host. Estimates of H were assessed in terms of total carbon gain by the parasite over a 9 week interval and these indicated that *A. amplexica* was the best provider of C (35.9g), followed closely by *S. formosa* (29.9g) and then *A. trachycarpa* (12.7g). Expressed in terms of proportional benefit, that is, the percentage of the net C gain in dry matter of the parasite afforded by C flow from xylem of the host, *A. amplexica* again turned out to be a better provider of C (57.9% of net C gain of parasite) than *A. trachycarpa* and *S. formosa* (values of 45.5% and 34.6%, respectively). It should be noted that the last mentioned host elicited much greater N gain than the other two, despite the low H rating on a percentage basis.

It is almost universally true that both aerial and root hemiparasites have substantially higher K concentrations than their hosts (Lamont and Southall 1982; Glatzel 1983; Schulze and Ehleringer 1984; Struthers *et al.* 1986; Seel and Press 1993; Pate 1995) and this was so for the *Santalum* : N₂-fixing host associations of this study (Figure 1), but, overtly not so for *Santalum* grown with the non-beneficial host *E. camaldulensis*. Barrett and Fox (1997) have suggested that *S. spicatum* may be capable of substantial independent K uptake through its own roots, but our results suggest that *S. album* competes ineffectively for K when grown with *E. camaldulensis* in a confined rooting medium. According to Glatzel (1983) and Seel and Press (1993), accumulation of K in xylem tapping hemi-parasites is a passive progressive enrichment process, with increases in the element proportional to transpiration rate of the parasite (Schulze and Ehleringer 1984; Kuppers *et al.* 1992). In our study transpiration rates per unit leaf area of *Santalum* grown with *E. camaldulensis* were just over half of those when grown on N₂-fixing hosts, a result in keeping with the conclusion suggested above (see Radomiljac *et al.* 1998d).

Consistent with data reported for *S. spicatum* by Struthers *et al.* (1986), the content of Na in foliage of *S. album* were very high compared with all other parts of the parasite, and generally much greater than in leaves and other parts of the associated host. High leaf Na contents compared with those of a host might be viewed as contributing to osmotic gradients, which coupled with high transpiration rates (Table 1), would ensure the efficient capture of water from the host (Struthers

et al. 1986). Fer *et al.* (1994) suggests that *Thesium humile* Vahl. (Santalaceae) has a high ability to take up Na direct from the soil and our study suggests the *Santalum* also has this ability. The K : Na ratios in foliage of *Santalum* plants grown on N₂-fixing hosts (0.55 – 1.19) in comparison with the low value of 0.27 when grown on *E. camaldulensis* and 0.13 when grown without a host, suggest K discrimination over Na is improved when grown in association with N₂-fixing hosts. The mechanism whereby this occurs would be worthy of further study.

Our study provides convincing evidence that certain hosts provide *Santalum* with minerals as well as N, and that the degree of benefit in respect of specific elements may be idiosyncratic of the host involved. This is indicated, for example, by the greater content of Ca in all parts of *Santalum* when in association with *A. trachycarpa*, a species that accumulated Ca more than 10 times the contents shown in other hosts. Ca contents in hemi-parasites have been used to distinguish between phloem and xylem feeding parasites (Ziegler 1976; Tsivion 1978; Lamont and Southall 1982; Struthers *et al.* 1986) due to Ca being relatively mobile in the xylem. As there is no lumen to lumen tracheary continuity between host and parasite in the haustoria of most root hemi-parasites (Rao 1942; Webb 1984; Pate *et al.* 1990a; Riopel and Timko 1995; Tennakoon and Pate 1996b), xylem transfer from host to parasite must involve the apoplastic pathway through haustoria cell walls (Coetzee and Fineran 1987; Kuo *et al.* 1989; Pate *et al.* 1994), with the additional possibility that parenchymatous cells at the haustoria interface with the host xylem might facilitate transfer of selectively absorbing host xylem solutes, and then release these and derived solutes to

the xylem of the parasite (Radomiljac *et al.* 1998c). The low Ca content in all *Santalum* plant parts when grown with *E. camaldulensis* is consistent with there being little such xylem-derived benefit in terms of Ca uptake from this host. This hypothesis is confirmed by the findings that contents in *Santalum* plant tissue of the phloem mobile P, K, Mg and Na showed little resemblance to that of its associated host for all associations.

During the course of the studies reported in this and earlier papers (Radomiljac *et al.* 1998b, c, d), we have employed a wide range of indirect criteria as possible mechanisms for assessing potential benefit to the parasite. A selection of those is listed in Table 4 and ranked in order of relative accuracy as predictors of biomass gain of the parasite by the final harvest of the study. The analysis ascribes very high r² ratings (0.87 – 0.99) to N and C increments of the parasite over the last 9 weeks of growth, N concentrations in shoot and leaf dry matter of the parasite, and its final leaf area. All of these parameters are likely to be highly correlated with growth performance. Near equal ratings also apply to final K content of foliage (r² = 0.90) and somewhat surprisingly to Na increment of *Santalum* over the final 9 weeks of growth (r² = 0.94). All other criteria listed in Table 4 carry r² ratings in a much lower range (0.03 – 0.60) and are accordingly discarded in terms of yield prediction.

Using various combinations of the highly significant predictive attributes listed above, the stepwise regression procedure was tested for predicting final dry weight of *Santalum* in the various associations. Four such regressions are shown in Table 5, one (A) achieving an r² rating of 0.99 after two steps, one (B) after three, and the other two (C and D) after four. While

Table 4. Growth and compositional criteria relative to single pot cultured associations of *Santalum album* with leguminous and a eucalypt host and the relative usefulness of these in prediction of final dry weight of the parasite. The model $y = b_0 + b_1 \text{factor}$. r² is used to calculate respective coefficients of determination.

| Factor | Santalum dry weight at 33 weeks (g plant ⁻¹) | | | |
|--|--|---------|----------------|-------|
| | b0 | b1 | r ² | p |
| N concentration of <i>Santalum</i> shoot dry matter (%) ^b | 24.8 | 104.5 | 0.99 | 0.002 |
| <i>Santalum</i> root : shoot ratio ^a | 673.5 | -722.1 | 0.99 | 0.006 |
| Increment in total N of <i>Santalum</i> over 9 week period (24 – 33 weeks) (g plant ⁻¹) ^c | 31.9 | 102.2 | 0.99 | 0.002 |
| <i>Santalum</i> leaf area (cm ²) ^a | 14.6 | 0.03 | 0.98 | 0.011 |
| Increment in total C of <i>Santalum</i> over 9 week period (g plant ⁻¹) ^c | 23.7 | 2.9 | 0.98 | 0.012 |
| Increment in total Na of <i>Santalum</i> over 9 week period (g plant ⁻¹) ^d | 76.7 | 461.8 | 0.94 | 0.033 |
| K content of foliage of <i>Santalum</i> (mg g ⁻¹) ^c | -236.1 | 578.9 | 0.90 | 0.050 |
| N content of foliage of <i>Santalum</i> (mg g ⁻¹) ^c | -145.2 | 162.6 | 0.87 | 0.065 |
| C:N ratio of organic solutes of <i>Santalum</i> xylem sap ^f | 285 | -4.04 | 0.60 | 0.224 |
| N concentration of <i>Santalum</i> xylem sap (mgN/ml) ^f | -1.789 | 2.674 | 0.51 | 0.283 |
| Increment in total K of <i>Santalum</i> over 9 week period (g plant ⁻¹) ^d | 99.1 | 295.7 | 0.42 | 0.350 |
| Total number of haustorial attachments to host ^g | 45.2 | 2.03 | 0.41 | 0.363 |
| Host use efficiency (parasite DW / host DW) ^a | 81.6 | 42.5 | 0.35 | 0.412 |
| N use efficiency in photosynthesis (mmol s ⁻¹ mg ⁻¹ N) ^h | 11.7 | 7091 | 0.33 | 0.428 |
| <i>Santalum</i> shoot : root ratio ^a | -56.221 | 130.594 | 0.24 | 0.515 |
| Na content of foliage of <i>Santalum</i> (mg g ⁻¹) ^c | 285.9 | -99.5 | 0.21 | 0.539 |
| Increment in total P of <i>Santalum</i> over 9 week period (g plant ⁻¹) ^d | 125.9 | 2431 | 0.19 | 0.563 |
| Total dry weight of host root (g plant ⁻¹) ^a | 203.7 | -0.73 | 0.12 | 0.645 |
| N concentration of host shoot dry matter (%) ^b | 91.5 | 68.9 | 0.07 | 0.732 |
| Total dry weight of host shoot (g plant ⁻¹) ^a | 172.7 | -0.15 | 0.03 | 0.843 |
| C:N ratio of organic solutes of host xylem sap ^f | 180.5 | -0.62 | 0.03 | 0.843 |

^a, Radomiljac *et al.* (1998b); ^b, Table 1 of this paper; ^c, Table 2 of this paper; ^d, Figure 4 of this paper; ^e, Figure 2 of this paper; ^f, Radomiljac *et al.* (1998c); ^g, Figure 1 of this paper; ^h, Radomiljac *et al.* (1998d);

obviously highly successful, the regression approach of B and D carries the major disadvantage of using information from destructive harvests of the parasite and, in the cases of increments of C and N, a requirement for two such sequential harvests. This would clearly limit the practical value of procedure in the field. An almost equally useful procedure would be to restrict parameters used in the regression to minimally destructive assays of foliage or xylem sap as in the case for A and C for specific elements such as N, K and possibly Na, since all of these were particularly well correlated with *Santalum* yield. With the prospect of large scale commercial enterprises cultivating *S. album* in north Western Australia, using the primary and some of the intermediate hosts suggested in this series of papers, effective procedures for monitoring growth, and models for predicting yield and quality of wood will become of great value, particularly since protocols suggested for plantation management have so far been tested only for relatively short time spans in early life of hosts and parasite.

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References

Barrett, D. R. and Fox, J. E. D. 1997. *Santalum album* : Kernel composition, morphological and nutrient characteristics of pre-parasitic seedlings under various nutrient regimes. *Annals of Botany* **79**: 59-66.

Cechin, I. and Press, M. C. 1993. Nitrogen relations of the sorghum-*Striga hermonthica* host-parasite association: growth and photosynthesis. *Plant, Cell and Environment* **16**: 237-247.

Coetzee, J and Fineran, B. A. 1987. The apoplastic continuum, nutrient absorption and plasmatubules in the dwarf mistletoe *Korthalsella lindsayi* (Viscaceae). *Protoplasma* **136**: 145-153.

Fer, A., Russo, N., Simier, P., Arnaud, M-C. and Thalouarn, P. 1994. Physiological changes in a root hemi-parasitice angiosperm, *Thesium humile* (Santalaceae), before and after attachment to the host plant (*Triticum vulgare*). *Journal of Plant Physiology* **143**: 704-710.

Gjerum, L., Fox, J. E. D. and Ehrhart, Y. (eds.). 1995. *Sandalwood seed nursery and plantation technology. Proceedings of a regional workshop for Pacific Island countries, 1-11 August, 1994.* UNDP/FAO South Pacific Forestry Development Programme. RAS/92/361, Noumea, New Caledonia, 303 pp.

Glatzel, G. 1983. Mineral nutrition and water relations of hemiparasitic mistletoes: a question of partitioning experiments with *Loranthus europaeus* on *Quercus petraea* and *Quercus robur*. *Oecologia* **56**: 193-201.

Table 5. Examples of a stepwise regression procedure for accurately predicting *Santalum* dry weight.

| | b0 | b1 | b2 | b3 | r ² | p |
|---|----------|---------|---------|---------|----------------|-------|
| (A) | | | | | | |
| <i>Santalum</i> DW = b0 + b1Nsxs ¹ | -1.789 | 2.674 | - | - | 0.51 | 0.283 |
| <i>Santalum</i> DW = b0 + b1Nsxs + b2N%sdm ² | 14.787 | 0.291 | 98.952 | - | 1.00 | 0.005 |
| (B) | | | | | | |
| <i>Santalum</i> DW = b0 + b1Ninc ³ | 31.9 | 102.2 | - | - | 0.99 | 0.004 |
| <i>Santalum</i> DW = b0 + b1Ninc + b2Cinc ⁴ | 35.9 | 142.3 | -1.16 | - | 0.99 | 0.054 |
| <i>Santalum</i> DW = b0 + b1Ninc + b2LA ⁵ | 47.6 | 185.9 | -0.03 | - | 1.00 | 0.004 |
| <i>Santalum</i> DW = b0 + b1Ninc + b2Cinc + b3LA | 47.9 | 184.8 | 0.16 | -0.03 | 1.00 | - |
| (C) | | | | | | |
| <i>Santalum</i> DW = b0 + b1Nsxs | -1.789 | 2.674 | - | - | 0.51 | 0.283 |
| <i>Santalum</i> DW = b0 + b1Nsxs + b2K%sl ⁶ | -288.007 | 0.765 | 501.207 | - | 0.93 | 0.267 |
| <i>Santalum</i> DW = b0 + b1Nsxs + b2N%sl ⁷ | -205.132 | -2.974 | 288.948 | - | 0.98 | 0.134 |
| <i>Santalum</i> DW = b0 + b1Nsxs + b2K%sl + b3N%sl | -230.254 | -2.027 | 188.473 | 203.767 | 1.00 | - |
| (D) | | | | | | |
| <i>Santalum</i> DW = b0 + b1RSratio ⁸ | 673.5 | -722.1 | - | - | 0.99 | 0.002 |
| <i>Santalum</i> DW = b0 + b1RSratio + b2N% ⁹ | 38.2 | -14.9 | 102.3 | - | 0.99 | 0.058 |
| <i>Santalum</i> DW = b0 + b1LA + b2N% | 25.4 | -0.002 | 109.5 | - | 0.99 | 0.004 |
| <i>Santalum</i> DW = b0 + b1RSratio + b2N% + b3LA | 2753.3 | -2999.9 | -8.9 | -0.11 | 1.00 | - |

¹ N concentration of *Santalum* xylem sap (mgN/ml)

² N concentration of *Santalum* shoot dry matter (%)

³ Increment in total N of *Santalum* from week 24 to 33 of parasite : host association (g plant⁻¹)

⁴ Increment in total C of *Santalum* from week 24 to 33 of parasite : host association (g plant⁻¹)

⁵ *Santalum* leaf area (cm²)

⁶ K content of foliage of *Santalum* (mg g⁻¹)

⁷ N content of foliage of *Santalum* (mg g⁻¹)

⁸ *Santalum* root : shoot ratio

⁹ N concentration of *Santalum* shoot dry matter (%)

- Hamilton, L. and Conrad, C. E. (eds.). 1990. *Proceedings of the symposium on sandalwood in the Pacific; April 9-11, 1990*. General Technical Report, PSW-122, Pacific Southwest Research Station, Forest Service, US Department of Agriculture, Honolulu, 84 pp.
- Havel, J. J. and McKinnell, F.H. 1993. *A review of the commercial management of sandalwood*. Paper presented at the 15th Biannual Conference of the Institute of Australian Foresters. 19 pp.
- Hocking, P. J. 1980. Aspects of the mineral nutrition of the Western Australian Christmas Tree (*Nuytsia floribunda* (Labill.) R. Br.), with special reference to the main root. *Australian Journal of Botany* **28**: 385-392.
- Hocking, P.J. and Fineran, B. A. 1983. Aspects of the nutrition of the root parasitic Loranthaceae. In: *Biology of Mistletoes* (M. Calder, P. Bernhardt eds.). New York: Academic Press, 229-258.
- Kitson, R. E. and Mellon, M. G. 1944. Colorimetric estimation of Phosphorus as Molybdovanadophosphoric acid. *Ind. Eng. Chem. A. E.*, **16**: 379.
- Kuppers, M., Kuppers, B. I. L., Neales, T. F. and Swan, A. G. 1992. Leaf gas exchange characteristics, daily carbon and water balances of the host/mistletoe pair *Eucalyptus behriana* F. Muell. and *Amyena miquelii* (Lehm. Ex Miq.) Tiegh. at permanently low plant water status in the field. *Trees* **7**: 1-7.
- Kuo, J., Pate, J. S. and Davidson, N. J. 1989. Ultrastructure of the haustorial interface and apoplastic continuum between host and the root hemiparasite *Olex phyllanthi* (Labill.) R. Br. (Olacaceae). *Protoplasma* **150**: 27-39.
- Lamont, B. and Southall, K. J. 1982. Distribution of mineral nutrients between the mistletoe, *Amyema preissii* and its host, *Acacia acuminata*. *Annals of Botany* **49**: 721-725.
- Linder, S. and Rook, D. A. 1984. Effects of mineral nutrition on carbon dioxide exchange and partitioning of carbon in trees. In: *Nutrition of Plantation Forests* (G. D. Bowen, E. K. S. Nambiar eds.). Academic Press. pp 211-236.
- McKenzie, H. A. and Wallace, H. S. 1954. The Kjeldahl determination of nitrogen: a critical study of digestion conditions – temperature, catalyst and oxidising agent. *Australian Journal of Chemistry* **7**: 55-70.
- McKinnell, F. H. (ed.). 1993. *Sandalwood in the Pacific Region*. Proceedings of a symposium held on 2 June at the XVII Pacific Science Congress, Honolulu, 1991. Australian Centre for International Agricultural Research proceedings No. 49, 43 pp.
- Nambiar, E. K. S. 1990. Interplay between nutrients, water, root growth and productivity in young plantations. *Forest Ecology and Management* **30**: 213-32.
- Pate, J. S. 1995. Mineral relationships of parasites and their hosts. In: *Parasitic Plants* (M. C. Press, J. D. Graves eds.). Chapman and Hall, London, pp. 80-102.
- Pate, J. S., Kuo, J. and Davidson, N. J. 1990a. Growth, resource allocation and haustorial biology of the root hemiparasite *Olex phyllanthi* (Olacaceae), with special reference to the haustorial interface. *Annals of Botany* **65**: 425-436.
- Pate, J. S., Pate, S. R., Kuo, J. and Davidson, N. J. 1990b. Growth, resource allocation and haustorial biology of the root hemiparasite *Olex phyllanthi* (Olacaceae). *Annals of Botany* **65**: 437-449.
- Pate, J. S., True, K. C. and Kuo, J. 1991. Partitioning of dry matter and mineral nutrients during a reproductive cycle of the mistletoe *Amyema linophyllum* (Fenzl.) Tieghem parasitising *Casuarina obesa* Miq. *Journal of Experimental Botany* **42**: 427-439.
- Pate, J. S., Woodall, G., Jeschke, W. D. and Stewart, G. R. 1994. Root xylem transport of amino acids in the root hemiparasitic shrub *Olex phyllanthi* (Labill.) R.Br. (Olacaceae) and its multiple hosts. *Plant, Cell and Environment* **17**: 1263-1273.
- Press, M. C., Shah, N., Touhy, J. M. and Stewart, G. R. 1987. Carbon isotope ratios demonstrate carbon flux from C4 host to C3 parasite. *Plant Physiology* **85**: 1143-1145.
- Radomiljac A. M., Shea, S. R., McKinnell, F. H. and McComb, J. A. 1998a. Potential for irrigated tropical forestry in northern Western Australia. *Australian Forestry* **61**: 70-75.
- Radomiljac, A. M., McComb, J. A. and McGrath, J. F. 1998b. Intermediate host influences on the root hemi-parasite *Santalum album* L. biomass partitioning. *Forest Ecology and Management*, **113**: 143–153.
- Radomiljac, A. M., McComb, J. A., Pate, J. S. and Tennakoon, K. U. 1998c. Xylem transfer of organic solutes in *Santalum album* L. (Indian sandalwood) in association with legume and non-legume hosts. *Annals of Botany* **82**: 675-682.
- Radomiljac, A. M., McComb, J. A. and Pate, J. S. 1998d. Gas exchange and water relations of the root hemi-parasite *Santalum album* L. grown in association with legume and non-legume woody hosts. *Annals of Botany*, **83**: 215–224.
- Radomiljac, A. M., McComb, J. A. and Shea, S. R. 1998e. Field establishment of *Santalum album* L. – the effect of the time of introduction of a pot host (*Alternanthera nana* R. Br.). *Forest Ecology and Management* **111**: 107-118.
- Rai, S. N. 1990. Status and cultivation of sandalwood in India. In: *Proceedings of the symposium on sandalwood in the Pacific; April 9-11, 1990* (L. Hamilton, C. E. Conrad eds.). General Technical Report PSW-122, Pacific Southwest Research Station, Forest Service, US Department of Agriculture, Honolulu, pp. 66-71.
- Rao, L. N. 1942. Parasitism in the Santalaceae. *Annals of Botany* **6**: 131-151.
- Riopel, J. L. and Timko, M. P. 1995. Haustorial initiation and differentiation. In: *Parasitic Plants* (M.C. Press and J. D. Graves eds.). Chapman and Hall, London. pp. 39-79.
- Schulze, E-D. and Ehleringer, J. R. 1984. The effect of nitrogen supply on growth and water-use efficiency of xylem-tapping mistletoes. *Planta* **162**: 268-275.
- Seel, W. E. and Press, M. C. 1993. Influence of the host on three sub-Arctic annual facultative root hemiparasites. I. Growth, mineral accumulation and above-ground dry matter partitioning. *New Phytologist* **125**: 131-138.
- Seel, W. E., Cooper, R. E. and Press, M. C. 1993. Growth, gas exchange and water use efficiency of the facultative hemiparasite *Rhinanthus minor* associated with hosts differing in foliar nitrogen concentration. *Physiologia Plantarum* **89**: 64-70.
- Srinivasan, V. V., Sivaramakrishnan, V. R., Rangaswamy, C. R., Ananthapadmanabha, H. S. and Shankaranarayana, K. H. (eds.). 1992. *Sandal* (*Santalum album* L.). Indian Council of Forestry Research and Education, Dehra Dun, 233 pp.

- Struthers, R., Lamont, B. B., Fox, J. E. D., Wijesuriya, S. and Crossland, T. 1986. Mineral nutrition of sandalwood (*Santalum spicatum*). *Journal Experimental Botany* **37**: 1274-1284.
- Stoneman, G. L. and Dell, B. 1993. Growth of *Eucalyptus marginata* (Jarrah) seedlings in a greenhouse in response to shade and soil temperature. *Tree Physiology* **13**: 239-52.
- Subbarao, N. S., Yadav, D., Padmanabha, A., Nagaveni, Singh, C. S. and Kavimandan, S. K. 1990. Nodule haustoria and microbial features of *Cajanus* and *Pongamia* parasitised by sandal (sandalwood). *Plant and Soil* **128**: 249-56.
- Systat. 1992. *Systat for Windows. Version 5 Edition*. Evanston, IL: Systat, Inc., 750 pp.
- Taide, Y. B., Babu, L. C. and Abraham, C. C. 1994. Influence of host species on the initial growth and development of sandal (*Santalum album* Linn.) *Indian Journal of Forestry* **4**: 288-292.
- Tennakoon, K. U. and Pate, J. S. 1996a. Effects of parasitism by a mistletoe on the structure and functioning of branches of its host. *Plant, Cell and Environment* **19**: 517-528.
- Tennakoon, K. U. and Pate, J. S. 1996b. Heterotrophic gain of carbon from hosts by the xylem-tapping root hemiparasite *Olex phyllanthi*. *Oecologia* **105**: 369-376.
- Tennakoon, K. U., Pate, J. S. and Stewart, G. R. 1997a. Haustorium-related uptake and metabolism of host xylem solutes by the root hemiparasitic shrub *Santalum acuminatum* (R. Br.) A. DC. (Santalaceae). *Annals of Botany* **80**: 257-264.
- Tennakoon, K. U., Pate, J. S. and Fineran, B. A. 1997b. Growth and partitioning of C and N in the shrub legume *Acacia littorea* in presence or absence of the root hemi-parasite *Olex phyllanthi*. *Journal of Experimental Botany* **48**: 1047-1060.
- Tennakoon, K. U., Pate, J. S. and Arthur, D. 1997c. Ecophysiological aspects of woody root hemiparasite *Santalum acuminatum* (R. Br.) A DC. and its common hosts in south Western Australia. *Annals of Botany* **80**: 245-256.
- Tsivion, Y. 1978. Physiological concepts of the association between parasitic angiosperms and their hosts - a review. *Israel Journal of Botany* **27**: 103-121.
- Veenendaal, E. M., Abebrese, I. K. and Walsh, M. F. 1996. Root hemiparasitism in a West African rainforest tree *Okoubaka aubrevillei* (Santalaceae). *New Phytologist* **134**: 487-493.
- Webb, A. 1984. *Structure and function of the haustorium of Santalum spicatum (R. Br.) A. DC.*. Honours Thesis, Murdoch University, Perth.
- Ziegler, H. 1976. Nature of transported substances. In: *Encyclopedia of Plant Physiology Transport in Plants. I. Phloem Transport*. (M. H. Zimmerman and J. A. Milburn eds.). Springer-Verlag, Berlin, pp. 59-100.