School of Environmental Biology

Aspects of Early Growth and Host Relationships in *Santalum album* L.

Thomas Lion

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Abstract

Early survival of *S. album* is generally poor and is mainly dependent on early connections between *S. album* and hosts. By the connection, organic compounds, minerals and water are possibly transferred from host to *S. album*. It is assumed that plants frequently found with *S. album* include 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 parasitism that can be tolerated by particular host communities.

In this study, early growth and host relationships in *S. album* L. were conducted in the Curtin Field Trial Area (FTA) at Bentley, Perth, Western Australia to investigate germination, the relationship between *S. album* and hosts, the relationship between *S. album* and the single best host in a sterile medium and observations on potential hosts of *S. album*.

S. album seeds from three different batches (Bangalore, India; the CALM trials at Kununurra and the Field Trial Area) were germinated in the glass house in August 1998 in seed trays containing sterilised coarse sand on heat mats at 25^{0}C. Germination results showed differences in seed source, conditions and treatments. This is in terms of germination percentage, seed size, and days to first and final germination. The larger seed had greater germination percentage, and medium seed germination first.

The relationship between *S. album* and hosts (*Alternanthera* sp., *Acacia acuminata* and *Citrus* rootstock) in 10 treatments (control sets, single host sets and combination host sets) was examined. Hosts affected *S. album* seedling growth as early as 28 days. There were significant differences in *S. album* seedling growth rates when associated with single and combinations of hosts. The most beneficial effect came from the relationship between *S. album* and *Alternanthera* sp. as a single host. The combination of hosts *Alternanthera* sp. and *Citrus* rootstock made greater contributions to growth and survival of *S. album* seedlings than other combinations or single hosts.

Foliar nutrients were used to examine any effects on the relationship between *S. album* and single best host in three sets (*S. album* alone; *S. album* with *Alternanthera* sp. and *Alternanthera* sp. alone). Each set consisted of 7 treatments (control; N, P, K; N, P, K and trace elements; Ca; Mg; Fe; and trace elements). It was shown that *S. album* can survive at least 3 months without *Alternanthera* sp. in the sterile medium but in poor health. Supplementary nutrient solutes did not affect growth of *S. album* seedlings. Early growth of *S. album* seedlings depends on cotyledon nutrients and later some essential nutrients are transferred from *Alternanthera* sp.

Observations on *S. album* hosts were conducted among planted trees in the Curtin FTA. Six species of host plants in healthy condition were found associated with *S. album*. *Acacia saligna, Casuarina glauca, Gompholobium tomentosum, A. rhodophloia, Ehrarta calycina* and *Hardenbergia comptoniana* appear to be good hosts for *S. album*. The jam tree *A. acuminata* and the Queensland mulga *A. aneura* had earlier been good hosts but after some 15 years of parasitism, many of them were dead. *Citrus* trees had also been killed early, indicating they would not be good hosts in the long-term. Self-parasitism was found in *S. album* and it was also found to parasite the related species *S. spicatum*.

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1. Introduction

The genus *Santalum* belongs to the family Santalaceae. This is characterised by species with the parasitic habit and includes shrubs, small evergreen trees and climbers. The genus has high economic, cultural and medicinal values. Sandalwood products have three major uses: carvings, incense and oil. The fragrant wood is used in producing ornaments, cabinets and chests; incense for religious rites; and the oil for perfume and medicines. It has been used in toiletry, its oil has antipyretic, antiseptic, antiscabietic and diuretic properties, and is also used for the treatment of some diseases, such as migraine, gonorrhoea, cystitis, dysuria and diseases of the urinary tract. Sandalwood has nearly 15 different names in the Indian languages, "chandana(a)" being the Hindi name. In Indonesia it is named "Cendana", "shrikhand" in Nepal, while in Sanskrit it is named "malayaja" (Rai 1990).

The main reason for the economic and cultural values of sandalwood is the oil contained in its timber, especially in its heartwood. It has the highest oil content, with about 6-7 percent. Oil is obtained from the heartwood of the stem and the root of the tree. It is a colourless or pale yellow liquid with a sweet and persistent woody odor, containing not less than 90% free alcohols by weight. The alcohols are principally of the sesquiterpene group and are referred to collectively as santalol. There are two major components: α-santalol and β-santalol; while a-santalene, b-santalene and santalyl acetate also contribute in a minor way to the overall odor. The heartwood colour varies from yellow through brown to deep chestnut-brown. Light brown wood contains the most oil (2.5-2.6%), santalol in this oil is about 85-90%. Yellow wood contains 1.3-3.5% oil, santalol about 90%; dark brown contains less than 2.5% oil, santalol in this oil is about 75-85%; while deep chestnut brown contains 2.5% oil with less than 85% santalol (Applegate *et al.* 1990).

The family Santalaceae has 37 genera; most of the genera are small trees. About 20 genera have four or fewer species and 10 genera are monotypic. Barrett and Fox (1995) indicate that Santalaceae can occur in various climates; species can be found in tropical, sub-tropical and temperate regions of the New and Old World.

The genus *Santalum* has 28 taxa, consisting of 15 species, and 13 varieties (Barrett and Fox 1995). Neil (1990) indicates that confusion exists over the taxonomy of some of these species due to variations in appearance and habits. For example, *Santalum insulare* from French Polynesia and *S. marchionense* from Marquesas may be varieties of the same species. The majority of sandalwood species grow on islands of the Pacific Ocean. The genus *Santalum* grows naturally in regions with a rainfall range between 200-3800 mm and an elevation range between 0-2600 m.

Sandalwoods can grow in warm desert regions (Australia), through seasonally dry monsoon climates (India, eastern part of Indonesia and Vanuatu), to sub tropical climates with almost uniform rainfall (Hawaii and New Caledonia). Sandalwood species are present in southern India, Indonesia, New Guinea, Australia and islands of the Pacific Ocean (Applegate *et al.*1990).

In Australia, endemic species of sandalwood consist of *S. acuminatum* (R.Br.)A.DC. (quandong), *S. lanceolatum* (R.Br.) (plum bush), *S. murrayanum* (Mitch.) C. Gardner (bitter quandong), *S. obtusifolium* (R.Br.) and *S. spicatum* (R.Br.)A.DC. (Western Australian sandalwood). These species, except *S. obtusifolium*, grow in Western Australia. *S. obtusifolium* has a distribution from southeast Queensland through eastern New South Wales to Far Eastern Victoria (George 1984). Only one non-endemic species (*S. album* L. or Indian sandalwood) grows in the Northern Territory. It grows in sandy soil and is associated with mangrove communities near small coastal waterholes. It may have been introduced from Asia a long time ago (George 1984).

Indian sandalwood grows naturally in both southern India and Indonesia. There are two contradictory hypotheses of the origin of Indian sandalwood. The first hypothesis states that *S. album* was introduced to India from Timor a long time ago (Rajagopal Shetty, 1977). The second hypothesis suggests that it is endemic to India based on Indian culture, literature and ethos (Rai, 1990). The tree has a wide range of geographical distribution and geographical conditions compared to that of other *Santalum* species. In India, sandalwood tolerates a rainfall range between 300-3000 mm and an elevation range from 0-700 m. In Indonesia, it occurs in a rainfall range of 800 - 1800 mm, at an elevation range from 0-2000 m (Applegate *et al.* 1990).

S. album can grow in and tolerate a variety of soil types depending on geographical location. Soil acts as the substrate for sandalwood growth and the quality and characteristics of the soil can affect growth. Knowledge of the characteristics of a particular soil is needed for understanding what plants can exist. Different components can affect water retention e.g. fine soil particles (clays) and organic soils hold more water than coarse sands (McCloud and Bula, 1973). Compactness can affect root development. Some soils have relatively fine sand at the surface and particles become finer further into the ground (Knight, 1965). In India, sandalwood grows on free-draining red loams (pH range of 6-6.5). Occasionally it is found on sandy soils associated with laterites (Doran and Turnbull, 1997). In West Timor, *S. album* is found on very stony, grey clay and red loam soils that are derived from coral parent material. It has a pH range of 8-9 (Applegate *et al.* 1990). In India, *S. album* is capable of growing in different textural classes of soils including sand, clay, laterite, loam and black-cotton soil. Even very poor and rocky soils can support Indian sandalwood (Rai, 1990), but it avoids very wet conditions.

The morphological characteristics of *S. album* vary, based on geographical location. Indian sandalwood can reach a maximum height of 20 m and girth of 1.5 m (Doran and Turnbull 1997). The bark is tight, rough and fissured, being dark grey to black in colour while being reddish in the fissures. There are many differences in sandalwood bark between young and old trees; young tree bark is reddish brown, red inside and smooth while old tree bark is rough with deep vertical cracks. Indian sandalwood has a hard and very close grained, oily heartwood, while the sapwood is white and scentless. Furthermore, the heartwood is yellow to brown and aromatic. The branchlets are slightly angular-striate. Sandalwood has leaves opposite or whorled. Leaves are light green, opposite, sometimes alternate, occasionally ternate, ovate or ovate-lanceolate, glabrous and shining above and glaucous below. The lamina is 25-70 mm long and 15-40 mm wide; venation is reticulate; margins are flat or slightly recurved; and the petiole is 2-ribbed and 5-15 mm long (George, 1984).

S. album starts flowering at age 3 years but does not produce viable seed until age 5. Some literature states that *S. album* trees can produce fertile seed at three or four years. Sandalwood seed should be more prolific and the proportion of fertile seed will increase with age until twenty years (Fox *et al.* 1995a). Flowering occurs twice per year, but there are different times of flowering based on geographical distribution. In

Western Australia flowering starts from December and mature seeds are produced in January; and flowering also occurs from June, with seeds maturing in August. In both India and Indonesia flowering is in March (seeds mature in April) and September (seeds mature in October) (Applegate *et al.* 1990). Different fruiting times between areas depend on environmental conditions and possibly genetic influence.

S. album has a bisexual flower that is unscented, with up to six small terminal and axillary panicles; the peduncle is about 4-11 mm long; and pedicels are less than 1 mm long. The receptacle is 2 mm long. There are four tepals (rarely 5 or 6) which are triangular to ovate, obtuse, 2 mm long, these can be red or green; four stamens (same number as tepals). The disc has prominent, ovate lobes. The style is short (2 mm long) and the stigma is small (3 lobed). The fruit contains one seed enclosed by a hard thin endocarp which is brown and smooth, and the albumen is white (George 1984).

Both seed crops in India are of similar size, about 6-7 mm in diameter with a thin fleshy exocarp about 1 mm (Applegate *et al.* 1990). There is evidence that the weight and size of *S. album* seeds in Timor tends to vary greatly between individual trees based on geographical location. There are relationships between diameter and weight of seeds. Fox *et al.* (1994) describe a strong positive linear relationship between the two. A 0.1-mm increase in diameter corresponds with an increase of 6.6 mg in seed weight.

In many plant species there is a relationship between seed size and germination (Brand, Fox and Effendi 1993). Factors that may affect the size of seeds include both genetical and environmental aspects. Little work appears to have been done on factors that affect seed size and weight of *S. album*. Larger seeds in Timor have been noted as having higher and faster germination rates than those of small seeds. Larger seeds in the weight range of 0.150-0.225 g have a success rate of 47.5%, taking 146 days to complete germination. This can be compared to that of small seeds (0.050-0.109 g). These seeds, with germination of 26.3% require 156 days to germinate (Brand, 1993).

S. album seeds have a post-drop dormancy period of 50-60 days due to the presence of the impenetrable outer coatings. For cultivation, fruit should be thoroughly defleshed immediately after collection from the tree by scoring while washing in water. After that, seeds should be well rinsed and then surface sterilised using a 10 % solution of sodium hypochlorite. At this stage some floating seeds can be discarded, as a high proportion of floaters will be infertile (Fox *et al.* 1994).

All seeds should be dried in a single layer in an airy, warm place but out of direct sunlight. After that, seeds should be dressed with fungicide, have naphthalene flakes added and than stored in a cool, dry place until required. Kagy (1987) reports that refrigeration can extend the period of viability of *S. album*. In *S. austrocaledonicum*, seeds maintain viability for 2-3 years. This procedure should reduce the length of dormancy exhibited by the seeds, and also reduce the chances of harmful bacteria affecting seedlings during the germination process. Cleaned seeds can further reduce the dormancy period and germination can occur from 9 days after sowing (Brand 1993, Fox *et al.* 1994).

Methods that have been employed for speeding up the germination process include soaking seeds in gibberellic acid or sulphuric acid. Sulphuric acid erodes the endocarp, making it thinner and thus increasing its permeability to water. Gibberellic acid is used to leach out chemical inhibitors from the seed causing a reduction in the dormancy period (Nagaveni and Srimathi, 1980).

In the germination stage, *S. album* seeds are influenced by a number of conditions such as time from collection, storage, germination medium and environmental conditions generally, especially temperature. The optimal temperature for germination of *S. album* is 25°C (Fox *et al.* 1994), while in *S. austrocaledonicum* optimum temperature is 25°C-27°C (Applegate *et al.*, 1990). Media used in the germination stage vary; in India, *S. album* seed is sown in sunken or raised beds (Rai and Kulkarni, 1986); in Australia seed trays are used, or for research trials petri dishes (Brand *et al.* 1993). In West Timor, individual pots are used (Surata, 1992) while in New Caledonia, the Centre Technique Forestier Tropical (CTFT) has developed a system of crushed coral beds, bottom heated to maintain a temperature of 25°C. After germination, seed is transferred into plastic tubes, and hosts are introduced later (Applegate *et al.* 1990).

As germinating seedlings are vulnerable to fungal or nematode attack, it is recommended to use regular treatments with fungicide and nematicides in both seedbeds and in potting mixes (Hirano 1977; Rai and Kulkarni 1986; Sivaramakrishnan *et al.* 1987). Typical fungal agents occuring as nursery diseases are

Fusarium oxysporium and species of *Mucor, Phytophthora* and *Pythium*. In India some fungi cause leaf spot infections: *Ascochyta santali, Asterina congesta, Mactophorina phaseoli, Oidium novital* and *Sphaedalomia santali* (Srinivasan *et al.* 1992).

Rai (1990) describes two types of seedbeds used in the nursery for raising sandalwood seedlings: sunken and raised beds. Seedbeds should be sprayed with the fungicide dithane Z-78 (0.25 %) once per 15 days to avoid fungus attack. To avoid nematode damage a 0.02 % Ekalux solution is suggested monthly. Media used in the germination stage are various depending on the local conditions. For species of sandalwood in Hawaii, vermiculite is used (Hirano 1977) whereas a mixture of sand and red earth is favoured in India (Rai and Kulkarni 1986). Crushed coral is used in New Caledonia (Kagy 1987) and a 1:3 mixture of sand and local soil in Timor (Surata and Fox 1989). In these media, seeds are spread uniformly and covered to about 1 cm (Rai, 1990). On the other hand Rai and Kulkarni (1986) noted that *S. album* seed planted 20 mm below the medium gives best results. Other reports suggest *S. austrocaledonicum* is placed 15 mm below medium (Fox *et al.* 1994) and *S. album* 5 mm below sand (Brand *et al.* 1993).

Germination trays should be maintained at 25°C. Sandalwood seedlings, generally have small white haustoria, on the young lateral roots. Sandalwood seedling roots can attach to minute rootlets of grasses and other surrounding plants. It is advantageous to grow seedlings in pots of pure sand. Those grown in earth and vegetable mould usually have abnormal, distorted and decayed roots (Barber 1902). Cotyledon resources may be sufficient to support plant development for up to a year, but: better growth and survival is obtained when plants have early haustorial attachments to host plants.

A seed of *S. album* is about the size of a pea; the embryo is linear and lies with the radicle pointed upwards. On germination the radicle protrudes and immediately turns downwards. The hypocotyl grows rapidly and soon forms a loop, the upper part of which rises above the surface. The seed coat eventually rots and falls off, but not before the food store in the cotyledons has been transferred to the hypocotyl. This part of the seedling becomes greatly swollen in its lower half, and the hypocotyl provides sustenance for the growing seedling until the roots are able to take on their natural function. The cotyledons have meanwhile broken off from the seed, the hypocotyl becomes erect, and the petioles of the cotyledons remain clearly visible as green stumps immediately above which new leaves are rapidly unfolded (Barber 1902).

Santalum species are hemi-parasites. The nature of the species necessitates formation of good haustorial connections between the sandalwood plant and its hosts for survival and growth to maturity (Sen Sarma 1977; Applegate *et al.* 1990; Srinivasan *et al.* 1992). Seedling growth can occur for about 6 months or more without hosts (Wijesuriya and Fox 1985; Widiarti 1989) when early growth depends on cotyledonary or endosperm nutrition. Some literature reports that N, K, Na, P, Ca, water and amino acids are transferred from hosts to sandalwood (Srimathi, Babu and Sreenivasaya 1961; Sen-Sarma 1977; Struthers *et al.* 1986) and variability in survival and growth is probably related to the success of haustorial connection (Rai 1990). Shade has a contribution in growth and survival of young sandalwood (Barrett and Fox 1994).

Early survival of cultivated *Santalum* species has generally been poor and mainly dependent on early host connections (Rai 1990). Host plants provide shade (Barrett and Fox 1994) as well as nutrition (Iyengar 1960). The time of haustorial development on sandalwood roots varies but haustoria are detectable in some *S.album* individuals at about 6 weeks from germination. It has been estimated that 97% of seedlings initiate haustoria, not necessarily making connections, over the course of the first year (Nagaveni and Srimathi 1985). The connection is xylem to xylem although there is also contact between parenchymatous tissues. Organic compounds (amino acids, sugars and enzymes, for example), minerals and water are possibly transferred from host to parasite. Some exchange from sandalwood to the host has also been noted (Kuijt, 1969). Chemical consequences of parasitic plants using different host species may deter herbivores feeding on the parasites (Marvier 1996).

It is assumed that plants frequently found with sandalwood include 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 parasitism that can be tolerated by particular host communities. Species known as excellent hosts in Western Australia of *S. spicatum* are *Acacia acuminata* and *A. aneura* (Fox 1997). On the other hand, a large number of *A. aneura* trees have died in the Curtin University FTA following the introduction of *S. album*. These were initially good hosts for this species also.

Whereas host preferences of epiphytic parasites can be observed directly, those of root parasitic trees can only be inferred without exploring root connections (Pennings and Callaway 1996). Marvier (1996) suggests that pot trials with host parasite pairs indicate direct negative effects on host growth. However, the growth of sandalwood is better when associated with some hosts rather than others (Rai 1990, Fox *et al.* 1996, Marvier 1996).

Several years ago a collection of 8 different cultivars of commercial *Citrus* trees at the FTA was eliminated by *S. album*. Is this genus particularly susceptible to death from parasitism or is it an exceptionally useful host?

The Indian sandalwood, formerly in abundance and the mainstay of a vigorous export market, is now scarce, especially in India and Indonesia. A programme of research into the biology and cultivation of *Santalum spicatum* (WA sandalwood) has been undertaken at Curtin University. In nature, WA sandalwood is considered a slow-growing tree. It requires a long time to reach a size where it can be harvested for its aromatic wood. Herbert (1925) observed extensive lateral roots that may run for more than 20 metres from the tree. Along the length of the lateral roots grow fine feeder roots (haustoria) that have the potential to parasitise suitable host roots.

Recent research on *S. album* suggests hosts may be categorised into three stages: pot or seedling host, intermediate host and long-term host. All three have a different function in plantation dynamics. The best pot hosts for different locations in association with *S. album* are *Desmanthus virgatus* in Timor (Fox *et al.* 1996), *Alternanthera nana* in Kununura (Radomiljac 1998), and *Cajanus cajan* in India (Rai 1990).

Early survival of the hemi-parasitic *Santalum* species in cultivation is poor (Loneragan 1990) and mainly dependent on early host connections (Rai 1990). In this project I study aspects of early growth and host relationship in *S. album*. The project is divided into four stages: germination, host attachment, effects of nutrients and finally, to discover the extent and range of parasitism demonstrated by established *S. album* in the FTA where a number of plants are attached. Plants used to study host attachment in this project were grown in one of ten treatments, each with 15 replicates. Treatment 1, the control was sandalwood alone; treatment 2: each pot had one S. *album* and one *Alternanthera* sp.; treatment 3: each pot contained a *S. album* and an *Acacia acuminata;* treatment 4: one *S. album* and one *Citrus* plant (rootstock); treatment 5: *S. album* + *Alternanthera* sp. + *A. acuminata* in each pot; treatment 6: *S. album* + *Alternanthera* sp. + *Citrus* rootstock; treatment 7 contained S. *album* + *Alternanthera* sp. + *A. acuminata* + *Citrus* rootstock in each pot; treatment 8 contained *Alternanthera* sp. as a control; treatment 9 contained *A. acuminata* as a control; and treatment 10 contained *Citrus* rootstock as a control. Two thousand seeds of *S. album* were used in the germination stage. From this, 273 germinants of *S. album,* 243 plants of *Alternanthera* sp. (host 1), 80 plants of *Acacia acuminata* (host 2) and 80 plants of *Citrus* rootstock (host 3) were used for the host relationships stage.

Objectives

1. To study the process of germination from seed to planting stage.
2. To determine whether combinations of hosts provide better nutrition than single hosts.
3. To investigate whether some hosts are preferentially parasitised or not.
4. To find out whether sandalwood parasitism diminishes the host.

2. Material and Methods

Four experiments were conducted to investigate aspects of early growth, particularly germination characteristics and host relationships, in *S. album* L. Firstly, a germination experiment was established to study the process of germination from seed to planting stage (Chapter 3). Secondly, a host experiment was used to determine whether combinations of hosts provide better nutrition than a single host (Chapter 4). Other aims were to show whether some hosts are preferentially parasitised or not and to find out whether sandalwood parasitism diminishes the host. Thirdly, an experiment using the best host sought to determine whether sandalwood requires its host as an obligatory source of nutrient elements (N, P, K, Ca, Mg, Fe and trace element) or whether it can utilise these elements, if administered directly to its own parts (leaves) (Chapter 5). Finally, a series of observations was made to discover the extent and range of parasitism demonstrated by established *S. album* in the Field Trial Area (Chapter 6).

Experiments were conducted at the Field Trial Area of the School of Environmental Biology at Curtin University of Technology. Three species of hosts were used: *Altenanthera* sp. (host 1), *A. acuminata* (host 2), and *Citrus* rootstock (host 3). Up to 2000 sandalwood seeds were germinated in the glasshouse to produce an adequate supply of *S. album* seedlings for use in the experiments.

Experiment 1. Germination

Two thousand seeds from two different populations of *S. album* were obtained. 1500 seeds (Indian sandalwood) were obtained from the Conservation and Land Management (CALM) Research Station at Kununurra. An older batch from Bangalore Forest Research Centre (Vanavikas 18^{K} Cross Malleswasam Bangalore 560 003 by registered letter RL 5209, 2 December 1992) had been stored at about 4^{0}C from early 1993. 700 seeds of the 1500 set were weighed individually on 1 to 3 August 1998.

Four benches (B1, B2, B3, B4) with heated beds (thermal growth panels) were prepared in the glasshouse. Forty seed trays, 35 by 30 by 4.5 cm, lined with paper towels, were filled with sterilised coarse sand to 50 mm and maintained at 25^{0}C on the heated beds in the glasshouse from 29 July 1998. Coarse sand had been sterilised in an electrical oven at 60^{0}C for 90 minutes.

On 4 August 1998, 2000 seeds were sown in the 40 seed trays, with each tray receiving fifty seeds in five lines (ten seeds per-line). The 700 weighed seeds were placed on bench 1 (ten trays) and bench 2 (four trays). Seeds in each tray were numbered 1 to 50. Seeds were positioned around 1 cm below the surface of the coarse sand.

All germination trays were drenched with previcur® fungicide (1.5ml in one litre of water) on 6 August 1998 and watered for the first time on 7 August 1998. Watering continued every 2 days until germinants were transferred to 50 mm diameter pots. These pots were filled with an FTA potting mix (2 parts coarse sand: 2 parts fine sand: 1 part compost). Transplanting took place when the hypocotyl reached a length of 10-20 mm. Daily inspections were made to check for signs of disease.

Germination dates were recorded for all seeds. Germination rates were calculated according to the following method:

$$\text{Germination rate} = \frac{(n_1t_1 + n_2t_2 + ... + n_xt_x)}{\sum n_{1.......x}}$$

Where:

n_1 = number of germinants on the first day of germination

t_1 = time (days) to the first germination

n_2 = number of germinants on the second day of germination

t_2 = time (days) to second germination

x = number of days to final germination

$\sum n_{1......x}$ = total number of seed germinated over the trial.

Other parameters were calculated as follows:

Germination Value (G.V.) = P.V. x M.D.G.

Where:

$$\text{P.V. (Peak Value)} = \frac{\text{Max.cumulative \% germination}}{\text{N}^0\text{days from start}}$$

$$\text{M.D.G. (Mean Daily Germination)} = \frac{\text{Final \% germination}}{\text{N}^0 \text{ days to final germination \%}}$$

The calculation of germination rate involved summing the total of germinants and total days from sowing and dividing by the total number of germinants. Peak value (P.V.) is the highest level of cumulative percentage germination divided by total days from the start. Mean daily germination (M.D.G.) is obtained by dividing final germination percentage by the total number of days taken for the final germinant. Germination value (G.V.) is peak value times mean daily germination.

Experiment 2. Host combinations

A set of 150 *S. album* seedlings was used with 75 plants of *Alternanthera* sp., 60 plants of *A. acuminata* and 60 plants of *Citrus* rootstock (Table 1). All sandalwood germinants were transferred from 50 mm diameter pots to 250 mm pots using the same mixture. In this experiment sandalwood seedlings and hosts (host 1, 2 and 3) were grown together in the same pot (250 mm diameter). The compost component of the potting mix was made using various organic materials (chicken manure, sheep manure, mushroom compost, jarrah sawdust, buzzel shavings, and iron sulphate). This was prepared in an electrically driven cement mixer with fertilisers added at mixing.

Table 1. Total number of plants (*S. album, Alternanthera* sp., *A. acuminata* and *Citrus* rootstock).

No	Treatment (plant combination)	Total number of plants used
1	*S. album* + no host	15 plants of *S. album*
2	*S. album* + *Alternanthera* sp.	30 plants (15 plants each)
3	*S. album* + *A. acuminata*	30 plants (15 plants each)
4	*S. album* + *Citrus* rootstock	30 plants (15 plants each)
5	*S. album* + *Alternanthera* sp. + *A. acuminata*	45 plants (15 plants each)
6	*S. album* + *Alternanthera* sp. + *Citrus* rootstock	45 plants (15 plants each)
7	*S. album*+ *Alternanthera* sp.+ *A. acuminata* + *Citrus* rootstock	60 plants (15 plants each)
8	*Alternanthera* sp. alone	15 plants of *Alternanthera* sp.
9	*A. acuminata* alone	15 plants of *Acacia acuminata*
10	*Citrus* rootstock alone	15 plants of *Citrus* rootstock

Alternanthera sp. was taken as cuttings. These were prepared on 23 September 1998 in the glasshouse to allow root development. After two weeks they were placed outside the glasshouse. *A. acuminata* was sown as seed into a seed tray. Seedlings were planted out on 8 September 1998. *Citrus* rootstock (60 plants) were purchased from a commercial nursery and replanted on 25 August 1998.

Table 2. Fertiliser components of the potting mix used.

No	Ingredient (g per cubic metre)	100 litres
1	86.7 g potassium nitrate	8.67 g
2	86.7 g potassium sulphate	8.67 g
3	1.134 kg single superphosphate	113.4 g
4	1.134 kg calcium carbonate lime	113.4 g
5	3.42 kg dolomite lime	342 g

When the *S. album* seedlings germinated and had four leaves or more, the seedlings from three different batches (table 3) were transplanted into pots on 24 October 1998 (treatment 1, 2); during 2 - 12 October 1998 (treatment 3); on 2 November 1998 (treatment 4); on 5 November 1998 (treatment 5, 6, 7) according to the experimental plan (Table 4).

Table 3. *S. album* seedlings from three different sources by treatments.

Treatment	Bangalore	FTA	Kununura	Total
1	1, 2, 3, 4, 5, 6 (6)	7 (1)	8, 9, 10, 11, 12, 13, 14, 15 (8)	15
2	3, 4, 5, 6, 7 (5)	-	1, 2, 8 to 15 (10)	15
3	5, 6, 10, 11, 12 (5)	1, 2, 7 (3)	3, 4, 8, 9, 13, 14, 15 (7)	15
4	1 to 5, 9, 10, 13 to 15 (10)	-	6, 7, 8, 11, 12 (5)	15
5	-	-	1 to 15 (15)	15
6	4 to 12, 14, 15 (11)	-	1, 2, 3, 13 (4)	15
7	1, 2, 13, 14, 15 (5)	7, 8 (2)	3 to 6, 9 to 12 (8)	15

S. album germinants together with hosts (treatments 1, 2, 3, 4, 5, 6, 7) and the individual hosts as control treatments (8, 9,10) were moved from the glasshouse to the hard-stand area outside on 2 November 1998. On 6 November 1998, all plants in this experiment were watered with fungicide. All treatment sets were watered every day using an automatic irrigation system for about 20 minutes.

Table 4. Date of planting of *S. album*, *Alternanthera* sp., *A. acuminata* and *Citrus* rootstock in ten treatments.

Treatment	Species of plants	Potting dates to prepare root development	Potting together
1	*S. album* (15)	26 September 1998	26 September 1998
2	*S. album* (15) *Alternanthera* sp. (15)	26 September 1998, 30 September 1998, 2 October 1998 23 September 1998	24 October 1998
3	*S. album* (15) *A. acuminata* (15)	26 September 1998 8 September 1998	2 October '98 (pot 1 - 4), 4 October '98 (pot 5 – 8), 5 October '98 (pot 9), 9 October '98 (pot 10-14) 12 October '98 (pot 15)
4	*S. album* (15) *Citrus* rootstock (15)	26 September 1998 25 August 1998	2 November 1998.
5	*S. album* (15) *Alternanthera* sp. (15) *A. acuminata* (15)	22 Oct. '98 (pot 1) 23 Oct.'98 (2-10,14-15) 27 Oct.'98 (pot 11, 12) 29 Oct. '98 (pot 13) 23 September 1998 8 September 1998	5 November 1998
6	*S. album* (15) *Alternanthera* sp. (15) *Citrus* rootstock (15)	23 October 1998 30 October 1998 25 August 1998	5 November 1998
7	*S. album* (15) *Alternanthera* sp. (15) *A. acuminata* (15) *Citrus* rootstock (15)	5 November 1998 30 October 1998 8 September 1998 25 August 1998	5 December 1998
8	*Alternanthera* sp. (15)	23 September 1998	23 September 1998
9	*A. acuminata* (15)	8 September 1998	8 September 1998
10	*Citrus* rootstock (15)	25 August 1998	25 August 1998

Height and total leaf numbers of *S. album* and the host for each treatment were measured immediately after planting (Table 5). Other measurements or assessment of heights and leaf numbers were continued for each host and *S. album* seedling fortnightly, for 6 weeks and thereafter, monthly to 22 weeks from potting together.

Table 5. Measurement dates of height and total leaf number of *S. album*, *Alternanthera* sp., *A. acuminata* and *Citrus* rootstock over the trial.

T	Potting together	2 weeks	4 weeks	6 weeks	10 weeks	14 weeks	18 weeks	22 weeks
1	24-10-98	7-11-98	21-11-98	5-12-98	5-1-99	5-2-99	5-3-99	5-4-99
2	24-10-98	7-11-98	21-11-98	5-12-98	5-1-99	5-2-99	5-3-99	5-4-99
3	24-10-98	7-11-98	21-11-98	5-12-98	5-1-99	5-2-99	5-3-99	5-4-99
4	2-11-98	16-11-98	30-11-98	14-12-98	14-1-99	14-2-99	14-3-99	14-4-99
5	7-11-98	21-11-98	5-12-98	19-12-98	19-1-99	19-2-99	19-3-99	19-4-99
6	7-11-98	21-11-98	5-12-98	19-12-98	19-1-99	19-2-99	19-3-99	19-4-99
7	7-11-98	21-11-98	5-12-98	19-12-98	19-1-99	19-2-99	19-3-99	19-4-99
8	24-10-98	7-11-98	21-11-98	5-12-98	5-1-99	5-2-99	5-3-99	5-4-99
9	7-11-98	21-11-98	5-12-98	19-12-98	19-1-99	19-2-99	19-3-99	19-4-99
10	2-11-98	16-11-98	30-11-98	14-12-98	14-1-99	14-2-99	14-3-99	14-4-99

T: treatment

The dimensions (mean and standard deviation) of height and total leaf number of *S. album* and hosts, when they were planted together can be seen in Table 6.

Table 6. Mean and standard deviation of height (cm) and leaf number of *S. album* and hosts at the start of the trial.

Plants	Group	N	Height Mean	Height SD	Leaf Number Mean	Leaf Number SD
Santalum album	1	15	5.23	0.96	5.60	1.12
	2	15	3.78	1.10	4.67	1.40
	3	15	4.43	1.53	5.20	1.52
	4	15	3.38	1.37	3.93	1.94
	5	15	2.50	0.94	1.80	0.86
	6	15	4.13	1.15	2.53	1.30
	7	15	2.85	0.78	2.00	1.36
Alternanthera sp.	2	15	6.59	1.44	66.27	15.71
	5	15	5.07	1.33	50.80	5.86
	6	15	6.01	2.04	47.80	4.07
	7	15	4.59	1.24	32.60	5.25
	8	15	7.96	2.02	73.07	19.99
Acacia acuminata	3	15	1.49	0.41	4.00	0.53
	5	15	1.10	0.18	4.33	0.62
	7	15	1.22	0.17	3.73	0.80
	9	15	1.54	0.33	4.40	0.91
Citrus rootstock	4	15	12.43	1.92	10.40	7.67
	6	15	23.53	25.31	21.13	7.99
	7	15	17.70	3.46	17.93	12.43
	10	15	20.03	3.64	12.53	6.40

Plants were grown until harvest, after 5.5 months (5 April 1999 for treatment 1, 2, 3; 14 April 1999 for treatment 4; 19 April 1999 for 5, 6, 8, 9, 10; and 16 May 1999 for treatment 7). Harvest measurements for *S. album* with hosts and in treatment 8, 9 and 10 included root architecture and number of haustoria present but not connected.

Experiment 3. Growth of hosted and unhosted *S. album* with plant nutrients supplied.

The third aspect of this project involved a similar setup to that for Experiment 2: the fertiliser regimes however, were different depending on the set within the trial and only one species of host was used. The potting medium used was coarse sand, thoroughly mixed in a cement mixer. This medium was used to provide a sterile base to constant effects of added nutrients. Each pot was labelled with individual seedling details. A total of 56 sandalwood plants and 56 host plants (*Alternanthera* sp.) was used. Sandalwood plants were taken from the Bangalore set (39 plants) and from the FTA batch-Bed 6 (17 plants). All germinants were taken from seed trays, sown on 16 December 1998 (Bangalore), and 18 December 1998 (FTA Bed 6). Plants were allocated to treatments in turn. It would have been desirable for plants to have been allocated at random. Four sandalwood plants in each sub-group consisted of 2 from Bangalore and 2 from FTA (Bed 6). Approximately 3 month-old sandalwood seedlings were set out on 26 March 1999 as follows:

1. Sandalwood without *Alternanthera* sp.: 28 plants. This set was divided into 7 sub groups (A1, A2, A3, A4, A5, A6, A7):
   4 pots (A1 as a control); 4 pots (A2: treated with N, P, K); 4 pots (A3: treated with N, P, K and trace elements); 4 pots (A4: treated with Ca); 4 pots (A5: treated with Mg); 4 pots (A6: treated with Fe); and 4 pots (A7: treated with trace elements).
2. Sandalwood with *Alternanthera* sp.: 28 plants. This set was divided into 7 sub groups (B1, B2, B3, B4, B5, B6, and B7):
   4 pots (B1 as a control); 4 pots (B2: treated with N, P, K); 4 pots (B3: treated with N, P, K and trace elements); 4 pots (B4: treated with Ca); 4 pots (B5: treated with Mg); 4 pots (B6: treated with Fe); and 4 pots (B7: treated with trace elements).
3. *Alternanthera* sp. without *S. album*: 28 plants. This set was divided into 7 sub groups (C1, C2, C3, C4, C5, C6, and C7):
   4 pots (C1 as a control); 4 pots (C2: treated with N, P, K); 4 pots (C3: treated with N, P, K and trace elements); 4 pots (C4: treated with Ca); 4 pots (C5: treated with Mg); 4 pots (C6: treated with Fe); and 4 pots (C7: treated with trace elements).

Four sandalwood plants in each sub-group (A, B and C) consisted of 2 from the Bangalore and 2 from the FTA batch (Bed 6).

At this stage both the host and the sandalwood sets were grown in a sterile medium. Nutrient solutions lacking in one of N, P, K; N, P, K + trace elements; Ca; Mg; Fe or trace elements were provided. The host (and sandalwood as a control, in each case) was given the missing nutrient on its leaves only. This enables the host to be fertilised independently of the sandalwood. From this trial it was possible to determine whether sandalwood requires its host as an obligatory source of these elements or whether it can utilise these elements, if administered directly to its own leaves. As much information was recorded as possible about the growth of the plants over the 20 weeks of the trial until harvest. Masses and haustorial numbers were obtained. Elemental concentrations were not measured due to shortage of material.

All nutrient solutes were applied as per the manufacture's recommendations: Mg (Mg micro: 60 ml per 100 litres water); Fe (Sequestrene 138 Fe: 0.05% solution or 10 ml per 20 litres water); Ca: Librel liquid Ca, chelated calcium 1% solution or 200 ml per 20 litres water; N, P, K: Aqua solution 16 ml per 20 litres water: N 23%, P 4.0%, K 18%; N, P, K + trace elements: Aqua solution 16 ml per 20 litres water: N 23%, P 4.0%, K 18%, Zinc 0.05%, Copper 0.06%, Molybdenum 0.0013%, Manganese 0.15%, Iron 0.06%, and Boron 0.011%; Trace elements: Fetrilon combination 0.05% solution or 10 ml per 20 litres water contains: 4.0% Zinc, 4.0% Iron, 3.0% Manganese, 1.5% Boron, 0.5% Cooper, 0.05% Molybdenum, 2.0% Magnesium and 2.8% Sulphur.

Liquids were made up for the 6 treatment sets and stored in 6 containers (20 litres each). Solution were dispensed from the container into 6 spray apparatus (500 ml each). Containers and spray apparatus were labelled as appropriate with nutrient solutes. The spray was applied through the plant leaves and all plant pots were moved about 7 to 10 metres from the experiment location, opposite to the wind direction. When spraying, measurements were taken first, followed by spraying of the relevant solution.

On 30 April 1999 all plants were treated for the first time by the appropriate nutrient solution. The treatments were continued every week (7 May, 14 May, 21 May, 28 May, 5 June, 12 June, 19 June, 26 June, 3 July, 10 July 1999) until the plants were aged approximately 20 weeks. The first measurement of sandalwood height and total leaf number was made on 18 April 1999. Further measurements were taken fortnightly until 4 weeks and thereafter monthly until 20 weeks (1 May, 15 May, 12 June, 10 July, 7 August and 5 September 1999). At the end of June 1999, all plant pots were moved from outside, into a plastic greenhouse because of a problem with birds (ravens attacking seedlings). At harvest, leaf and root areas were obtained with an electronic planimeter, as well as conventional dry weights. Sub samples of leaves and roots were measured from 2 pots (2 plants) of the 4 pots (4 plants) of each sub group. Leaves and roots were determined by measuring leaf area and root area after 20 weeks using computerized image analysis. Leaves and roots were placed in turn onto a computer scanner, and then scanned and saved on the computer. The image was then loaded into a NIH program on an LCIII Apple Macintosh computer. Each of the leaves and roots was measured by tracing the leaf or the root with a freehand tool. The results were exported into a text file.

Experiment 4. Observations on potential hosts of *S. album.*

A series of observations was conducted to discover the extent and range of parasitism in *S. album* trees at the Field Trial Area. Individual sandal trees from eight different beds were used to trace out the roots to connections from neighbours. They were: tree number 36 in Manning Road bed (line), tree number 8 in bed 6A, tree number 19 in bed 6, tree number 19 in bed 1A, tree number 9 in bed 3, tree number 8 in bed 7, tree number 3 in bed 9 and tree number 25 in bed 10.

Numerous *S. album* trees are located within the FTA and all are in a good healthy condition. There is a wide variety of potential hosts within the area in, and work was conducted to find out which plants *S. album* prefers. This would demonstrate which hosts are able to handle the strain of being parasitised.

The manner in which hosts were identified was by digging in an area at the base of a *S. album.* Haustoria of *S. album* were located and then the root that the haustoria were attached to was traced back to the plant from which it came. A judgement was then made of the health of the newly found host, using a ranking system of suitability of that host for parasitism by *S. album.* A record was kept of the host identity and a scoring system used for the amount of roots found. Plants that are poor hosts received a low ranking of 1 - 2, building up to an ideal host for *S. album,* that received a ranking of 9 - 10.

The Minitab statistical package was used to process the data. Processed results were printed as tables or illustrated as figures in the results.

3. Germination

Introduction

Germination is usually preceded by a variable period of time in which the seed remains dormant. Various factors can influence the period of seed dormancy. Collectively, these factors represent favourable conditions that may be required for the seedling to commence growth (Allaby 1992). Some species may have several requirements that must be met for seeds to germinate and grow. These requirements can be classified into two main categories: environmentally related, or intrinsic to the seed itself. Some seeds have specific morphological adaptations that influence seed movement into suitable germination microsites. For example, in some grass seeds the hygroscopic awns twist and untwist in response to humidity changes, thus moving the diaspore over the soil surface and, given the proper surface, drilling the diaspore into the soil (Peart 1979, Stamp 1989).

In natural conditions there may be a highly specific interaction between seeds and their environment. This can influence seed burial as individuals or the distribution of a species as a whole. The relatively high clay content of some soils render surfaces either loose or crumbly or that crack on drying (Peart and Clifford 1987). These soils may assist hygroscopic movement at the germinating stage, such that species with hygroscopically awned-diaspores predominate, presumably because their diaspores encounter more suitable microsites. On the other hand, high sand content in soil surfaces, or soils that are hard setting, have a tendency to form surface crusts, or are loose and single-grained, presenting surfaces whose condition is unsuitable for hygroscopically awned-species. Such soils may be dominated by unawned-species.

In the germination stage, seeds have syndromes that provide environmental cueing mechanisms that increase the probability of encountering conditions that are favourable for seedling growth and survival, essentially allowing seeds to disperse in time (Angevine and Chabot 1979). Under normal environmental conditions, seeds that are dormant are those that will not germinate readily and that must undergo after- ripening or embryo maturation, or be exposed to particular environmental stimuli (Baskin and Baskin 1989). Once seeds become active or nondormant, they must still experience the appropriate set of environmental conditions (light, temperature, and also soil moisture regimes) to permit germination to proceed. Seed loss can be influenced by effects of abiotic factors on biotic interactions, senescence and germination. Abiotic factors that can affect seed mortality include deep burial, crushing, abrasion, burning and waterlogging. Biotic factors can include such things as predation on fruits or seeds. Seed losses from various sources may have important consequences for the plant community, plant population dynamics and community composition (Hulse, Brown and Guo 1993) and also for succession processes (Davidson 1993). Predation, especially by seed predators differs during the different life stages of plants. Pre-dispersal predators of seed include insects from the orders: Diptera, Lepidoptera, Coleoptera and Hymenoptera (Crawley 1992).

Predation follows seed to the dispersal stage, where seeds may otherwise be in safe sites. Dispersed seeds may still not be safe from pathogens and larger predators; especially vertebrates (birds and mammals) that can find buried seeds. Furthermore, contamination of fungi or bacteria in the surface of the germination medium can cause seed death directly (through necrotic action) and indirectly via production of toxic metabolic wastes. In contrast, internally borne pathogens (some fungi and many viruses) often increase the metabolic activity of seed thus accelerating senescence (Burdon and Shattock 1980, Burdon 1987). In addition to causing seed death directly, fungal pathogens can decrease or stimulate germination (Clay 1987) and may result in altered seedling survival following germination (Crist and Friese 1993). Suspectibility to pathogen attack is possibly higher for physiologically active seeds than dormant seeds and may also increase as seeds age and membrane structure deteriorates (Burdon 1987).

Failed germination constitutes seed death soon after the process starts. We may distinguish between failed germination and seedling death because seedling death is usually evaluated only after seedling emergence. This potential ignores the death of numerous germinated seeds and underestimates seed bank losses. Antecedent conditions such as the effects of fungi (Clay 1987) or handling by animal dispersers (Vander Wall 1993) may increase the mortality of germinating seeds. On the other hand, consumption of germinating seeds by pathogens, predators, or granivores may also reduce survivorship.

Highly variable environmental conditions or unusual weather events can cause high mortality of germinating seeds (Cook 1979). Unusual weather conditions can also "miscue" the germination stage so that the timing of germination is inappropriate. Finally, seeds may arrive at microsites that provide the necessary conditions for germination but that are inadequate for survival and growth.

Other conditions that support the success of the germination stage are selection of an appropriate germination medium. Often, the preferred medium is that found in the local situation. Some media have been successfully treated for germination of *Santalum* seeds. For example, beds of a 1:3 sand to soil mixture that has been sprayed with nematicides and fungicides; another medium is a mix of sterile peat moss, vermiculite, and cinders (Applegate *et al.* 1990).

Selection of a germination medium is dependent on local availability of materials and on the climate conditions. Under different circumstances raised beds, seed trays, petri dishes or sowing into individual pots may have a place (Fox *et al.* 1994). Raised beds are favoured and well known in India, generally using a mixture of sand and red earth (Rai and Kulkarni 1986). In Australia and Timor, most reports are of using seed trays or individual pots with a 1:3 mixture of sand and local soil (Brand *et al.* 1993, Surata and Fox 1989). These media have been treated to eliminate pathogenic fungal attack. As sandalwood seed is especially susceptible, germination media must be treated with fungicides and nematicides (such as: Benlate®, Previcur®, Blitox®, Dithane-78®, Ekaline® and Thimet®). Applications may need to be continued over the duration of the germination process for a given batch of seed.

Maintenance of an appropriate level of moisture is important as this may influence the germination stage. Some researchers suggest that dry, cleaned, *S. album* seed is best stored in coarse sand with 2% moisture. This may yield a germination of 25-50% within 2 months. To maintain moisture, watering may be required, depending on climatic conditions: twice a day, once a day, once in two days or using automatic irrigation twice a day for twenty minutes (Rai and Kulkarni 1986; Surata 1992).

The depth of seed burial below the surface of the medium varies. In India *S. album* seed is planted at 20 mm depth, below coarse sand (Rai and Kulkarni 1986). In Australia it has been buried 5 mm below coarse sand (Brand *et al.* 1993).

It is reasonable to assume that optimum temperature ranges for germination vary with the species of sandalwood. For the tropical species of *Santalum*, temperatures in the mid to high 20's are reported. In Hawaii, sandalwood is germinated at 25°C (Hirano 1977); in New Caledonia (*S. austrocaledonicum*), germination is undertaken at 28°C-30°C (Kagy 1987); in Timor, ambient midyear temperature is suitable for good germination of *S. album* (Surata and Fox 1989); in Australia 25°C appears optimal for *S. album* (Brand *et al.* 1993) and this is obtained using controlled temperature cabinets or bottom heated trays in the glasshouse.

In sandalwood, germination starts at the time when the seed coat cracks and the radicle emerges. This descends into the soil followed by the loop of the hypocotyl emerging with the cotyledons retained in the seed and remaining below the surface of the medium. The lower portion of the hypocotyl then begins to swell as nutrients from the cotyledons are transferred to the enlarging part of the seedling. The seed is either carried from the ground where it will soon fall off or remain on the surface and rot away. Much work has been done on the germination of *S. album* in relation to breaking the dormancy of the seed, speeding up the germination process and the effect that seed size and weight has upon the germination process (Brand, 1993).

Results

There were differences in germination percentage (Table 7) between the three sources of *S. album* (CALM Kununurra batch, Bangalore batch and FTA batch - Bed 6) of the total of 2000 seeds used in the trial. The mean final germination of the CALM-Kununurra batch was only 6.5 %. In contrast, the other two sources gave higher germination. The Bangalore seed had significantly more germination than the other batches. The number of days to first germination ranged from 24 days to 33 days. On the other hand the final germination was reached between 97 days and 150 days. The Bangalore and Kununurra seed germinated faster having over 20 % germination in 33 days whereas the FTA seed took 11 days longer. In contrast, all batches took about the same time to reach 40 % germination (48 days to 49 days), and 50 % (50-52 days, not shown in Table 7).

Table 7. Final percentage germination and the rate of germination from three batches of *S. album*. (Populations ranked in order of decreasing final percentage germination).

Population	No. of seeds	Final germ. (%)	Days to first germ.	Days to 10% of final germ.	Days to 20% of final germ.	Days to 40% of final germ.	Days to final germ.
Bangalore	400	18.50a	24	28	33	49	106
FTA Bed 6	100	10.00b	33	33	44	48	97
CALM Kununurra	1500	6.47c	24	28	33	49	150

Detailed germination data are provided in Appendix 1. From these, germination rate, germination value, peak value and mean daily germination were calculated (Table 8).

Comparison of calculated values from the three different batches indicated differences in germination rate (Table 8). The germination rate of the Bangalore batch was greater than the two other batches. The Bangalore batch also had highest values for germination value, mean daily germination and peak value.

Table 8. Mean percentage germination and other parameters for batches of *S. album* seeds incubated at 25°C.

Collection Site	Bangalore	CALM	FTA Bed 6
Total sandalwood seed	**400**	**1500**	**100**
Germination Rate	10.83	3.69	5.66
Peak Value	0.38	0.14	0.15
Mean Daily Germination	0.17	0.04	0.10
Germination Value	0.07	0.01	0.02

A sub set of 700 seeds from the Kununurra batch was weighed to 4 decimal places using a Sartorius® balance. These seeds were then divided into three groups according to their weights with the medium weight class being 0.1750 < 0.2000 g. These seeds were sown in trays, each with 50 seeds, and placed on two benches B1 (10 trays); B2 (4 trays). Few seeds germinated (Table 9). Detailed results are in Appendix 2.

Table 9. Total number of *S. album* seed sown, total number of seeds germinated, total days for the first and final germination, and percentage germination of Kununurra *S. album* by weight grouping.

Weight group (gram)	No. of seeds	No. of seeds germinated	Total days for germination	Percentage germination
< 0.1749	221	2	98 - 117	0.90
0.1750 – 0.1999	242	8	29 – 148	3.30
> 0.2000	237	9	44 – 126	3.80

The smallest size group had least germination and took longer to commence. The heavier seed had slightly more germination than the medium weight seed. The latter commenced germination soonest.

Discussion

Sandalwood seed germination is notoriously variable, levels of up to 70-80 % have been reported (Bailly 1986; Nasi 1995). Compared to those levels, germination of seed used in the present project was poor. It was necessary to use some relatively old seed due to an insufficient supply of fresh seed. However, the older seed had higher germination than the fresh seed, despite the inevitable loss of viability that must have occurred in storage of older material. The Kununurra seed was of unknown quality and this gave poorest results. It is possible that the Kununurra material had not been cleaned to the same standard or stored as well as the other batches, resulting in either some prolonged dormancy or earlier loss of viability.

Even though fungicide was applied to the seed germination trays, this treatment may not have provided complete protection from pathogenic agents, mainly fungi and bacteria. Part of the explanation for poor germination may also have been associated with my inexperience in handling sandalwood seed. For example, maintenance of adequate soil moisture in germination trays initially proved difficult as the coarse sand medium used, lost moisture rapidly. This necessitated frequent topping up with water, depending on glasshouse temperature conditions. The problem of trays drying out was overcome within the first few weeks by placing seed trays in white butchers' trays with some water in the bottom.

When seed are set out to germinate, germination does not begin for at least 2 weeks after sowing and may be spread over several months (Applegate *et al.* 1990). Fresh FTA seed took longest to start germination (33 days) whereas the Bangalore and Kununurra seed started at the same time, after 24 days. This difference may have been associated with some dormancy in the fresh seed and minimal dormancy in older seed. However, 40 % of the final germination of each batch had germinated by 48-49 days. Staggered germination is frequently mentioned in the literature and for experiments, more or less synchronised germination is generally desirable. Where a large number of seedlings are required over a short time-frame, sufficient seeds must be sown to allow for anticipated germination levels. The proportion germinating sooner may be enhanced by pre-treatment. Both nicking of the testa or soaking of seed in GAA can improve germination (Fox *et al.* 1995 a).

The 3 seed lots used in this project differed in origin and germination results were clearly affected by the batch. The effect of time from collection on seed viability has been studied in some sandalwood species. Fresh seed (~ 1 year) of *S. album* may have up to 84 % germination and this tends to decline steadily with time to ~ 20 % after 9 years storage at ambient temperatures (Applegate *et al.* 1990). McKinnell (1990) recommended that fresh seed, no more than 2 years old, be used for successful direct seeding. The optimum (best) storage method is cold storage at 4^0C, over silica gel

(Applegate *et al.* 1990; Fox *et al.* 1995 a). Seed in this environment can maintain a germination of 52 % after 9 years (Applegate *et al.* 1990).

Seed used in this experiment had been stored for differing periods of time from collection. Bangalore seed was 7 years old; Kununurra seed had been collected one year prior to use; and the FTA seed was fresh.

Fresh fruit of *S. album* generally has an initial dormancy period associated with presence of the outer coverings rather than to primary dormancy. It is recommended that fruit is completely defleshed on collection by washing well in water and drying in shade, prior to cool, dry storage (Nagaveni and Srimathi 1980, 1981). The Bangalore seed had received this treatment some 7 years earlier and had been stored in a sealed bag, in a refrigerator at ~ 4^0C thereafter. The FTA fruit used was hand-picked by me from a 12-year old tree in May-June 1998, 2 months prior to sowing. Fruits were soaked in water and rubbed to remove the outer pericarp and fleshy mesocarp. Seeds were extracted and dried briefly in shade prior to storage for two months at 20^0C before sowing. This treatment may not have been sufficient to totally remove dormancy, said to be of about 2 months (Rai 1990). However, as this batch gave higher germination than the 1-year old seed from Kununurra, it must be assumed that the latter material was of poorer quality. Precise conditions of collection, cleaning and storage for that seed lot are not available.

Mean seed weights of Timor *S. album* seed from 10 populations varied between 0.125 and 0.151 g (Brand 1993). The Kununurra seed used here, from Indian parentage, had seed one third heavier at 0.20 g. This is in line with the previous observation that Indian seed is about twice as heavy as Timor seed (Fox *et al.* 1995 a).

Light weight seed of *S. album* in Timor germinates less well than heavy and medium weight seed (Brand 1993; Brand *et al.* 1993). When the Kununurra seed was sorted into 3 weight classes, greater germination was obtained from the medium and heavy seed than the light weight material. This suggests that lighter seed may be less viable generally and better germination will be obtained if lighter-weight seed is not included.

Better results may have been obtained if seed had been nicked or soaked in GAA prior to setting out. One of these treatments is recommended for any future experiments involving production of large numbers of similar sized *Santalum album* seedlings.

Conclusion

Seed kept under different conditions produced differing levels of germination when exposed to the same laboratory procedure. We cannot conclude that one source of seed is the best. This condition is caused by differences among seed sources in relation to collection conditions and the type and length of storage.

Fresh seed dormancy may be lost if seed are kept for more than 2 months after collection. Seed held at 4^{0}C can retain at least 18 % viability with 7 years storage.

4. Relationship between *S. album* and hosts

Introduction

Species of sandalwood show marked differences in morphological features such as form, leaf size, bark appearance and fruit size. Species that grow into large trees are probably amongst the most valuable in the genus *Santalum*. Three species are known to produce root suckers. These are *S. album*, the main commercial species from India and Indonesia, *S. lanceolatum*, an Australian species and *S. paniculatum*, a Hawaiian species. An ability to produce root suckers has a bearing on the ease of reproducing the plant (Applegate *et al.* 1990). The hemiparasitic nature of sandalwood species necessitates good haustorial connections between sandalwood plants and host plants. The phenomenon of root parasitism as a characteristic of *S. album* was first described in India and the significance of parasitism in relation to cultivation of *S. album* in India became reasonably well-known by the turn of the century. However, the frequent failure to establish good plantations in India has been ascribed to insufficient appreciation of the dynamics involved in root parasitism (Rai 1990).

Sandalwoods are able to make use of many species as hosts. Some 113 species belonging to 53 genera are known as host plants of *S. album* in India. These include several species of each of the following genera: *Acacia, Paraserianthes, Pterocarpus* and *Terminalia*. Understorey species are also parasitised by *S. album*. These include species of *Carissa, Lantana* and *Randia* (Applegate *et al.* 1990). Rai (1990) suggests that good hosts for field plantations of *S. album* are: *Acacia nilotica, Casuarina equisitefolia, Dalbergia sisso, Melia dubia, Pongamia pinnata, Wrightia tinctoria*; while *Cajanus cajan* is recommended as a good primary host.

In Indonesia, some Solanaceae, mainly food plant species have been widely used as the conventional first-stage host (Hamzah 1976). These include *Capsicum frutescens* (chilli), *Solanum melongena* L. (eggplant) and *Lycopersicum esculentum* Mill. (tomato). The local people in Timor use *C. frutescens* as a host for *S. album*.

In Timor, many plant species have been screened to discover hosts that enhance survival and early growth of *S. album*. A small woody shrub, *Breynia cernua* (Poiret) Muell. is known to host sandalwood well in pots (Fox *et al.* 1995 b) and to stimulate greater height growth on *S. album* than Solanaceae. Height of sandalwood increased more when associated with *B. cernua* than the weedy shrub *Calotropis gigantea* R.Br. (Kharisma and Sutarjo 1988). However, it is inappropriate to use weedy species as cultivated hosts, despite an apparent affinity to sandalwood by the invasive, weedy *Lantana camara* L., the grassweed *Imperata cylindrica* (L.) P.Beauv. (fire-climax) and also the low shrub *Stachytarpheta jamaicensis* Vahl. (Hamzah 1976, Mindawati 1987, Widiarti 1989). Some researchers suggest that pot hosts for sandalwood be restricted to plants suitable for other purposes than their being good hosts. Hosts in the nursery stage vary depending on the place and the climatic conditions. For example, *Cajanus cajan* is used as a pot host in India (Rai 1990), *Alternanthera nana* in northern Australia (Radomiljac 1998) and *Desmanthus virgatus* in Indonesia (Fox *et al.* 1996), especially in Timor.

Growth can be defined as the increase in size of an organism by cell enlargement or cell division (Allaby 1992). Growth requirements vary between species and can be related to abiotic and biotic factors (Meissner 1994). Abiotic factors include habitat variation such as temperature, light, water, nutrients and rainfall while biotic factors include disease, competition and grazing. *S. album* as an obligate semi-parasitic tree needs a range of hosts. In early growth, *S. album* benefits from shade and host plants can provide shade as well as nutrition. The time of haustorial development on sandalwood roots varies but haustoria are detectable in some individuals at about 6 weeks from germination. *S. album* grows well when young, in the shade of bushes and clumps of vegetation, overhead shade is desirable only in very hot localities (Barrett and Fox 1994).

If *S. album* is grown with an efficient pot-host, early haustorial connection should enhance both nursery and field survival, and the parasite ought to grow faster than when grown without a host. Using pot-host species of *Desmanthus virgatus, Crotalaria juncea* or *Alternanthera* sp., *S. album* grows rapidly to a mean height >25 cm at <26 weeks from sowing, in Kupang, Timor (Fox *et al.* 1995 b).

Plant parasites can parasitise many different hosts and can, apart from epiphytes, attack multiple hosts simultaneously (Musselman and Mann 1978, Gibson and Watkinson 1989). Single *S. album* trees may parasitise variable numbers and species of hosts. The same general rule applies to other parasitic tree species in the genus. The balance between competitive and host effects is related to growth conditions (Watkinson & Gibson 1988). Do larger parasites directly diminish host growth? *Acacia aneura* is in poor condition near a number of *S. album* occurences at Curtin University FTA. Also a number of *Citrus* tree cultivars established at the same place were eliminated by *S. album*. Recent research on *S. album* pot hosts shows that *Alternanthera nana* increases *S. album* survival, height and diameter as well as maintaining a higher level of field persistence than other pot hosts (Radomiljac 1998).

In the present experiment, three species of interest were tested as pot hosts to investigate aspects of early growth of hosts and *S. album*. The three hosts used were *Alternanthera* sp., *A. acuminata* and *Citrus* rootstock. These three hosts are described below, based on Ross (1997) (Appendix 3).

Alternanthera sp.

Around 80 species have been recorded from warmer parts of the world, comprising this genus of annuals and perennials (and a few aquatics) allied to *Gomphrena*. Most of them are low sprawling or prostrate plants, with weak stems and simple leaves arranged in opposite pairs. Flowers are very small, concealed in dense clusters of chaff-like white or straw-coloured bracts that appear at the leaf nodes. At least one species of *Alternanthera* is used in Asia as a green vegetable and for medicinal purposes. At least 2 species are grown for their colourful summer foliage. Cultivation involves planting in humus-rich, well-drained soil in part-shade or full sun. Propagation is from cuttings or seed in spring. The cultivated variety used here was raised as cuttings, taken from a parent in a Bentley garden by Peter Mioduszewski. It is believed to be similar to the plant successfully used in Timor (Fox *et al.* 1996).

Acacia acuminata

Acacia Milld, is one of the largest genera in the family Leguminosae belonging to the subfamily Mimosoideae. The genus includes 1000-1200 species ranging from low-growing shrubs to tall trees. Most species are distributed in Australia and Africa

(Yingbao and Hongfeng 1994). Many of them have been introduced to other countries for economic and ornamental purposes. Some are deciduous but most are evergreen. Over 700 species are indigenous to Australia. They are also common in tropical and subtropical climates in Africa. African *Acacia* are characterised by vicious spines and are referred to as "thorn trees" (Ross 1997). Their leaves are bipinnate or are replaced by enlarged and flattened leaf stalks (phyllodes), which perform the function of photosynthesis. Flowers range from deep golden yellow to cream or white, and are crowded into globular heads or cylindrical spikes, often fragrant and producing abundant, bee- attracting pollen. Fruit are round or flattened pods. *A. acuminata* (common names: Raspberry Jam, Jam wattle, Jam) occurs widely in the wheatbelt of Western Australia where it is a preferred host of *S. spicatum* (Western Australian sandalwood) (Struthers *et al.* 1986). The association between *S. spicatum* and *A. acuminata* is characterised by the level of K, Na, Ca and other minerals taken by the parasite from the host (Struthers *et al.* 1986). It is also known as the most probable host of *S. murrayanum* (Barrett 1995). Seed for plants used here was collected at Westonia some 300 km east of Perth.

Citrus rootstock

The number of original wild species in this genus of evergreen small trees, originally native in the Southeast Asian region, is uncertain as many of the cultivated forms are probably of ancient hybrid origin following domestication, which took place mainly in China and India. Largely cultivated for their fruit, citrus plants are also attractive garden plants, with glossy evergreen leaves and fragrant flowers. Most species are frost tender but a few tolerate very light frosts; the lemon is the most cold resistant, especially when grafted onto the related *Poncirus trifoliata* rootstock, and the lime is the least cold resistant, doing best in subtropical locations. All *Citrus* can also be grown in pots, provided containers are large and the citrus are grown on dwarfing rootstocks. *Citrus* grow best on well-drained, friable, slightly acid, loam soil. They require full sun, regular watering and protection from wind, especially during summer. *Citrus* also need regular feeding, including large amounts of nitrogen and potassium for good fruiting. Pruning is done to remove dead, diseased and crossing wood. They are subject to a range of virus diseases. Many pests including scale, leaf miner, bronze orange bug, spined citrus bug and fruit fly can attack them. The plants used in this experiment were seedling rootstock individuals of *Poncirus trifoliata* purchased from a commercial nursery (Davids Garden Centre).

Results

The following results of treatments are divided into four sections. The first section explains the growth rate of *S. album* associated with hosts in seven treatments (*S. album* alone, *S. album* + *Alternanthera* sp., *S. album* + *A. acuminata*, *S. album* + *Citrus* rootstock, *S. album* + *Alternanthera* sp. + *A. acuminata*, *S. album* + *Alternanthera* sp. + *Citrus* rootstock, *S. album* + *Alternanthera* sp. + *A. acuminata* + *Citrus* rootstock). The second section deals with growth of *Alternanthera* sp. in five treatments (*Alternanthera* sp + *S. album*, *Alternanthera* sp. + *S. album* + *A. acuminata*, *Alternanthera* sp. + *S. album* + *Citrus* rootstock, *Alternanthera* sp. + *S. album* + *A. acuminata* + *Citrus* rootstock and *Alternanthera* sp. alone). The third section explains the growth rate of *A. acuminata* in four treatments (*A. acuminata* + *S. album*, *A. acuminata* + *S. album* + *Alternanthera* sp., *A. acuminata* + *S. album* + *Alternanthera* sp., and *A. acuminata* alone). Finally, the fourth section deals with growth of *Citrus* rootstock in four treatments (*Citrus* rootstock + *S. album*, *Citrus* rootstock + *S. album* + *Alternanthera* sp., *Citrus* rootstock + *S. album* + *Alternanthera* sp. + *A. acuminata* and *Citrus* rootstock alone).

The first section is divided into four parts. The first part describes the analysis and calculation of mean heights of *S. album* over the trial. The second part describes mean total leaf number of *S. album*. The third part summarises mean wet weight, dry weight and moisture of *S. album* at harvest. I have expressed % moisture as a proportion of total wet weight, for comparative purposes. Finally, the fourth part deals with the extent of haustoria development (*S. album* and hosts) over the trial. Each of sections 2, 3 and 4 are similarly divided into three parts. The first part in each section describes growth in terms of mean height of the hosts (*Alternanthera* sp. in section 2, *A. acuminata* in section 3 and *Citrus* rootstock in section 4). The second part deals with the total leaf number of hosts, and the third part describes the wet weight, biomass and moisture content of host plants.

1. *Santalum album*

S. album heights and total leaf numbers were measured on 8 occasions over the trial. The first measurement was made at the time of planting with the hosts (24 October to 7 November 1998). The next 3 were at fortnightly intervals until 6 weeks. After that, monthly records were taken until 5.5 months from planting. Calculation of wet weight, biomass and moisture were conducted at the time of harvest, at the end of May 1999.

1.1 Height

Segregation of plants by starting height was not undertaken due to problems in obtaining sufficient seedlings of *S. album* of the same size at the start of this experiment. This resulted in considerable differences between treatments in mean height of *S. album* at the first measurement. The control set with no host had tallest mean height at the start and it was not until 4 weeks from setting out that plants with *Alternanthera* sp. and *Citrus* rootstock as hosts had caught up (Table 10, Appendix 4). Little change in mean height of *S. album* seedlings took place over the first 10 weeks from planting out the trial (Figure 1). After 10 weeks both treatments with *Alternanthera* sp. + *Citrus* rootstock had equalled the control set in mean height. From 14 weeks onwards all 4 treatments including *Alternanthera* sp. as a host had grown taller than the control. From 10-22 weeks these 4 treatments remained best in terms of *S. album* mean height, and this more than doubled. The other 3 sets, without *Alternanthera* sp., continued to make little incremental height growth.

Table 10. Mean height (cm) of *S. album* in 7 treatments (n=15) over the trial from 24 October/7 November 1998 to the end of May 1999.

Set	Treatment (*S. album* + host)	Time in weeks							
		0	2	4	6	10	14	18	22
1	+ no host	5.23 a	5.55 a	5.98 a	6.27 a	6.96 ab	7.83 bc	8.59 c	9.47 c
2	+ *Alternanthera* cv	3.78 cd	4.05 c	4.37 d	4.79 d	5.94 bc	8.41 b	13.02 b	19.35 b
3	+ *A. acuminata*	4.43 b	4.74 b	5.15 bc	5.52 bc	6.15 bc	6.61 bc	7.01 c	8.07 c
4	+ *Citrus* rootstock	3.38 de	3.93 c	4.31 d	4.76 d	5.40 c	6.01 c	7.45 c	9.69 c
5	+ *Alternanthera* cv + *A. acuminata*	2.50 f	3.70 c	4.68 cd	4.91 cd	5.69 c	8.41 b	14.66 ab	21.04 b
6	+ *Alternanthera* cv + *Citrus* rootstock	4.13 bc	4.81 b	5.55 ab	5.98 ab	7.11 ab	11.03 a	18.67 a	27.64 a
7	+ *Alternanthera* cv + *A. acuminata* + *Citrus* rootstock	2.85 e	3.57 c	4.52 cd	5.11 cd	7.64 a	12.04 a	17.62 a	23.85 ab
F P		10.14 0.000 ***	5.10 0.000 ***	3.42 0.004 **	3.78 0.002 **	2.23 0.047 *	3.80 0.002 **	5.91 0.000 ***	8.59 0.000 ***

Means in a column with same letters are not significantly different (Tukey test at the 0.05 level).

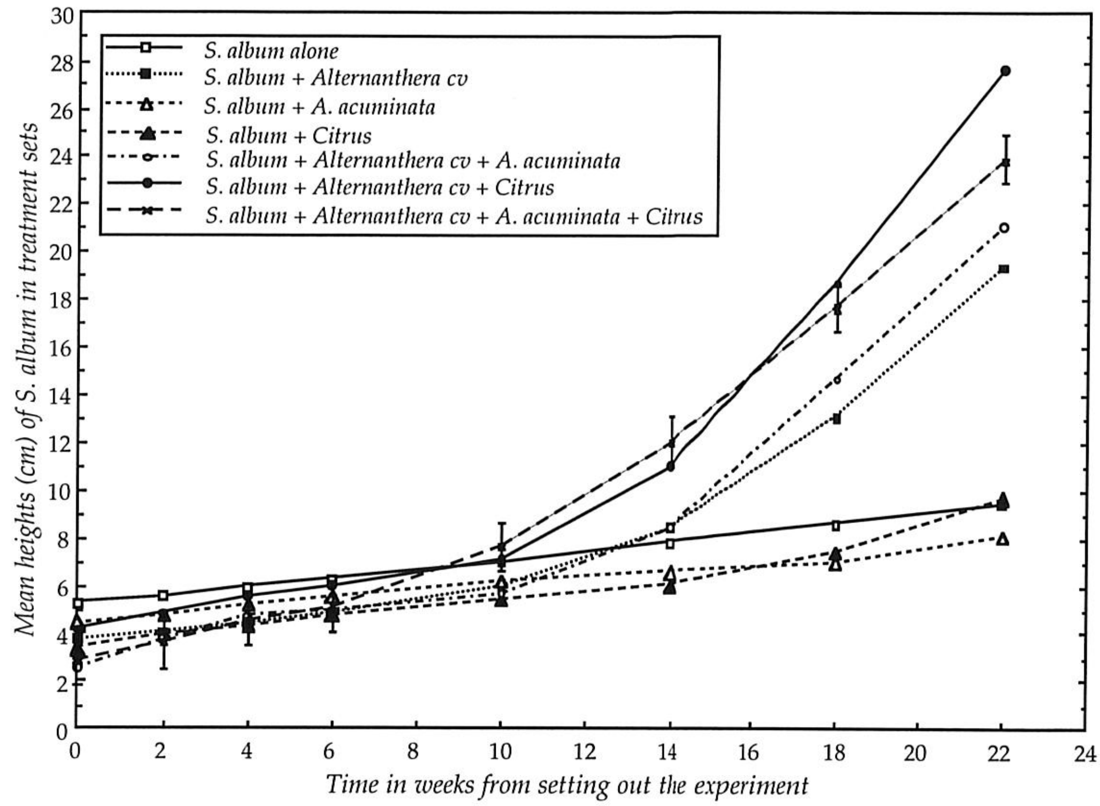


Figure 1. Mean height growth of *Santalum album* by treatment. Error bars are standard deviation.

By the end of the experiment significance testing revealed three groups among these 7 host treatments. Tallest *S. album* plants were those grown with *Alternanthera* sp. and *Citrus* rootstock. This set had sandalwood of mean height > 27 cm after 22 weeks, representing a mean weekly height increment of 1.07 cm. This treatment was not significantly different from sandalwood grown with all three hosts (0.95 cm week^{-1}), although *A. acuminata* made little contribution to these plants (Table 13 below). Shortest *S. album* plants were those grown without *Alternanthera* sp. Control plants with no host (0.19 cm week^{-1}) differed little from those grown with only *A. acuminata*. This latter set grew < 0.2 cm week^{-1} over the trial (0.17 cm week^{-1}) and their mean height was not significantly less than plants grown with only *Citrus* rootstock. However, these latter had mean growth of 0.29 cm week^{-1}. Other treatments were intermediate.

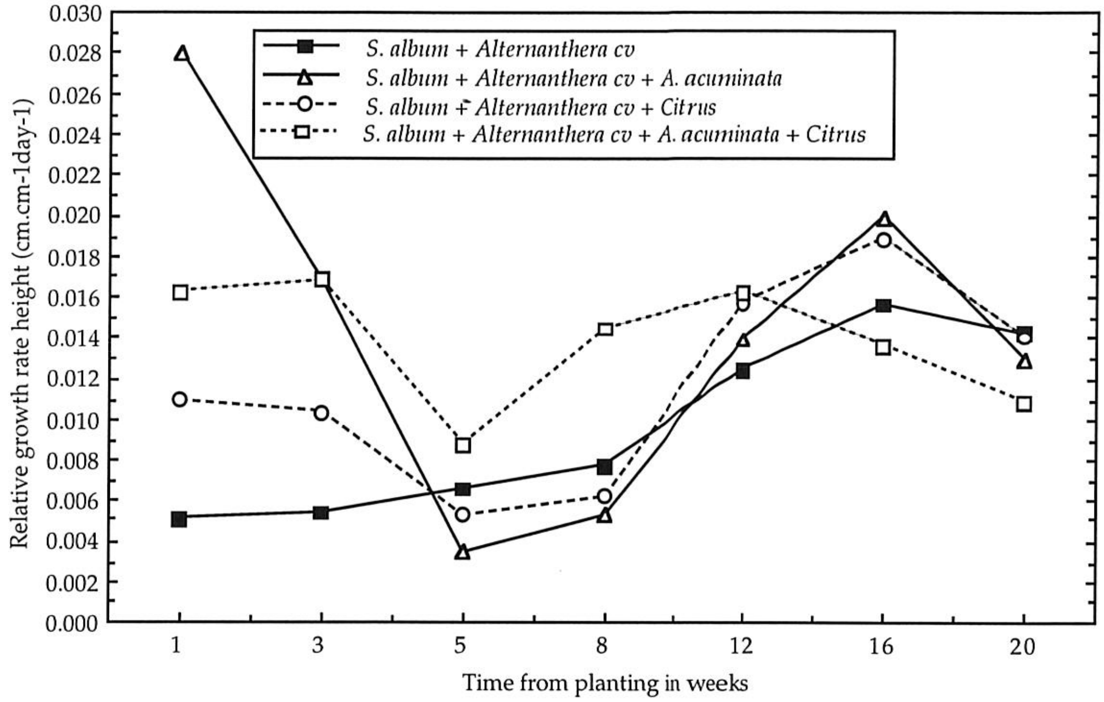
Relative growth rates (RGR) in height of *S. album* were calculated based on the formula:

$$RGR = \frac{\log eHt2 - \log eHt1}{t2 - t1}$$

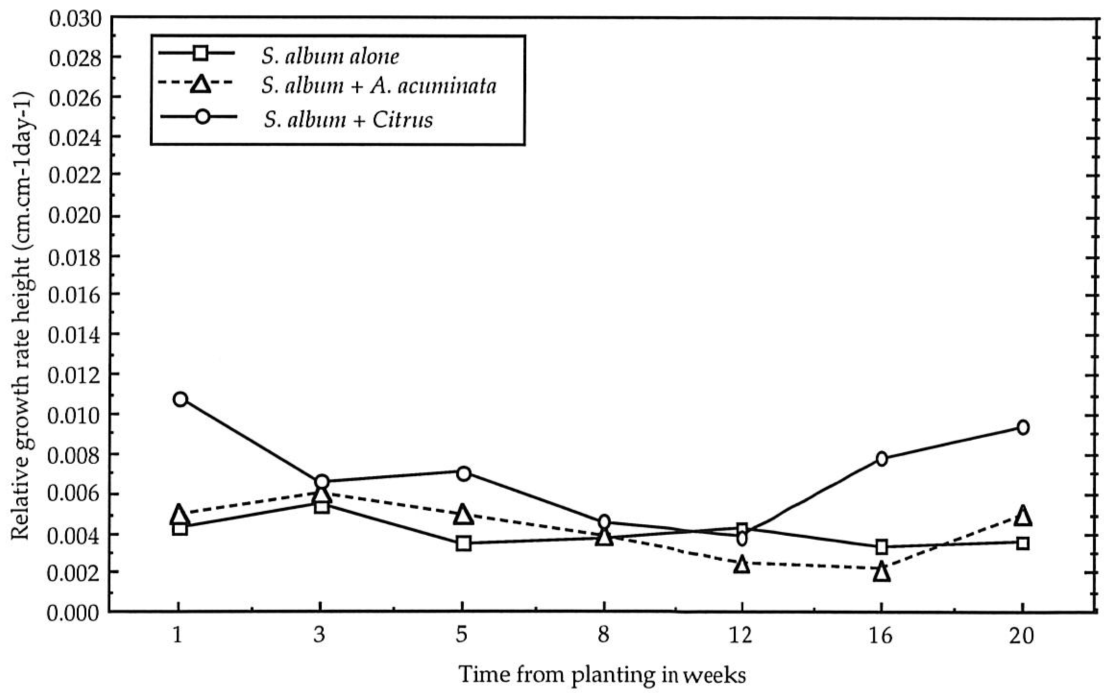
Mean heights of *S. album* in Table 10 were then transformed (log e) to find values for changes in mean height at 14 or 28 day intervals (Table 11, Figure 2).

Table 11. Calculated RGR values in cm. cm^{-1} day^{-1} for changes in mean height of *S. album* at 14 or 28 day intervals (Treatments as in Table 10).

Treatment	2-0 wk/14	4-2wk/14	6-4wk/14	10-6wk/28	14-10wk/28	18-14wk/28	22-18wk/28
1	0.0042	0.0054	0.0034	0.0037	0.0042	0.0033	0.0035
2	0.0050	0.0054	0.0065	0.0077	0.0124	0.0156	0.0142
3	0.0049	0.0060	0.0049	0.0039	0.0025	0.0021	0.0050
4	0.0108	0.0066	0.0070	0.0045	0.0038	0.0077	0.0094
5	0.0280	0.0168	0.0035	0.0053	0.0139	0.0199	0.0129
6	0.0109	0.0103	0.0053	0.0062	0.0157	0.0188	0.0140
7	0.0162	0.0168	0.0087	0.0144	0.0162	0.0136	0.0108



a. Relative growth rate height ($cm.cm^{-1}day^{-1}$) of *S. album* with *Alternanthera* sp.



b. Relative growth rate height ($cm.cm^{-1}day^{-1}$) of *S. album* without *Alternanthera* sp.

Figure 2. Relative growth rate in height ($cm.cm^{-1}day^{-1}$) of *S. album* by treatment sets.

1.2 Total leaf number

At setting out, mean leaf number on *S. album* seedlings varied from 1.8 in the set with *Alternanthera* sp. and *A. acuminata* to 5.6 in the set with no host (Table 12, Appendix 5). Mean total leaf number of *S. album* in all treatments steadily increased except for a decline (leaf fall) in the control from 11.5 to 9.5 at age 18 weeks. Total leaf numbers dramatically increased from 18 weeks in treatments with two or three hosts suggesting those plants may have made satisfactory haustoria attachments between 14 and 18 weeks from the start (Figure 3).

As with heights, there were significant differences in leaf number at the start of the experiment (Table 12). By 4 weeks treatment leaf numbers had evened up, with no significant differences between four treatments. By 14 weeks, the control plants were amongst those sets with poorest leaf numbers.

Table 12. Mean total leaf numbers of S. *album* in 7 treatments (n=15) over the trial from 24 October/7 November 1998 to the end of May 1999.

	Treatment (*S. album* + host)	Time in weeks							
		0	2	4	6	10	14	18	22
1	+ no host	5.60 a	7.33 a	8.20 a	9.27 a	11.47a	11.53 b	9.53 c	11.33c
2	+ *Alternanthera* cv	4.67 b	6.13 b	7.20 ab	8.07 b	10.27ab	13.33 ab	15.33 bc	22.60 bc
3	+ *A. acuminata*	5.20 ab	6.27 b	7.27 ab	8.07 b	9.47b	10.93 b	11.27c	13.33c
4	+ *Citrus* rootstock	3.93 c	5.60 b	6.40 b	7.33 b	9.80 b	11.60 b	12.60 c	15.93c
5	+ *Alternanthera* cv + *A. acuminata*	1.80 d	4.60 c	7.07 b	8.07 b	10.40ab	15.07 a	27.33 a	48.13a
6	+ *Alternanthera* cv + *Citrus* rootstock	2.53 cd	4.60 c	6.27 b	7.07 b	9.53 b	14.60 a	22.67ab	43.47a
7	+ *Alternanthera* cv + *A. acuminata* + *Citrus* rootstock	2.00 d	4.00 c	6.67 b	7.40 b	11.60a	16.07 a	23.80 ab	38.13 ab
F P		**18.92 0.000 *****	**6.49 0.000 *****	**1.81 0.104 NS**	**2.20 0.049 ***	**1.60 0.155 NS**	**2.29 0.041 ***	**2.35 0.036 ***	**2.64 0.020 ***

Means in columns with the same letters are not significantly different (Tukey test at the 0.05 level).

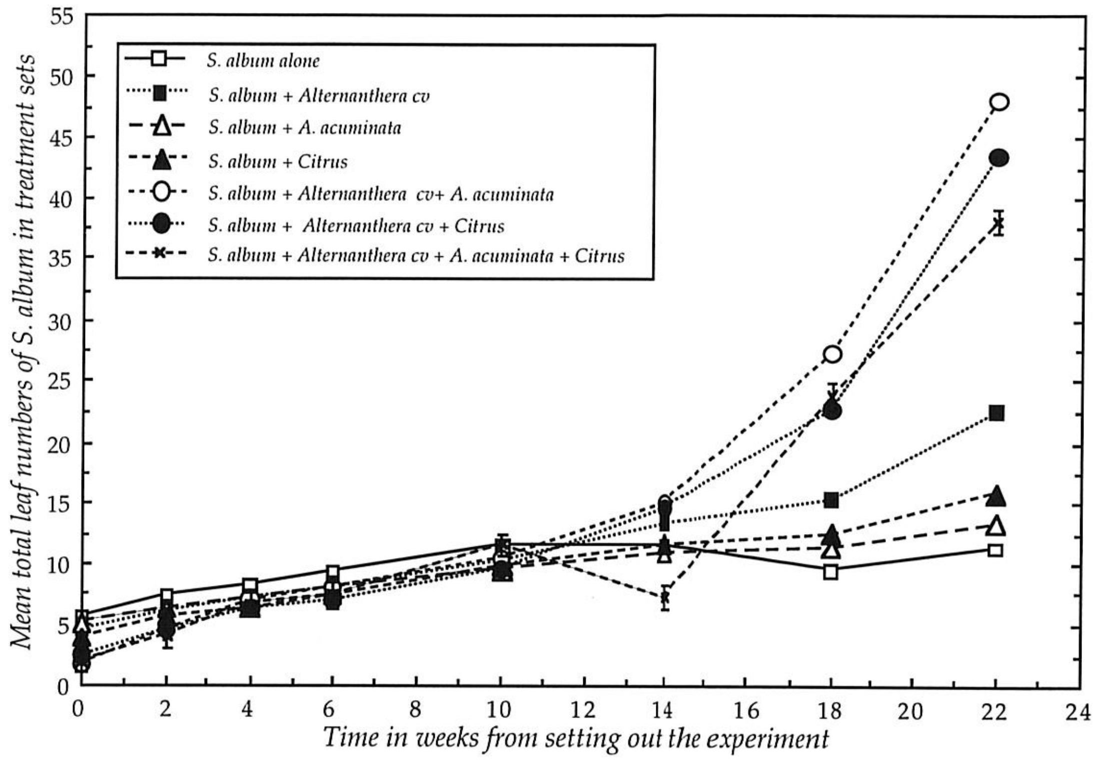


Figure 3. Mean total leaf number of *S. album* by treatment sets. Error bars are standard deviations.

Comparison of mean height and leaf number in Table 10 and 12 suggests that taller *S. album* tended to have more leaves. It has often been reported that there is a spurt in growth when haustorial connections are successfully made and the parasite is drawing materials from the host. To examine whether attained height depends on leaf numbers, the mean values of all 7 treatments at 8 measurement dates were paired and tested for regression (Figure 4). Significant linear association was found at $p<0.001$. Height increases with leaf number ($r^2=0.897$).

When each treatment set is examined separately for linear regression, the relationship is significant for all treatments at $p=0.001$ for all except *S. album* alone (Table 13).

Table 13. The relationship between *S. album* height and leaf number (n=8 measurement means, in each treatment using simple linear regression.

Treatment	Mean height (cm) =	r^2
+ no host	1.953 + 0.542 leaf number	0.595 *
+ *Alternanthera* cv.	-2.046 + 0.914 leaf number	0.990 ***
+ *A. acuminata*	1.973 + 0.444 leaf number	0.990 ***
+ *Citrus* rootstock	1.038 + 0.500 leaf number	0.947 ***
+ *Alternanthera* cv + *A. acuminata*	1.856 + 0.414 leaf number	0.989 ***
+ *Alternanthera* cv + *Citrus*	2.171 + 0.610 leaf number	0.980 ***
+ *Alternanthera* cv + *A. acuminata* + *Citrus*	1.117 + 0.622 leaf number	0.984 ***

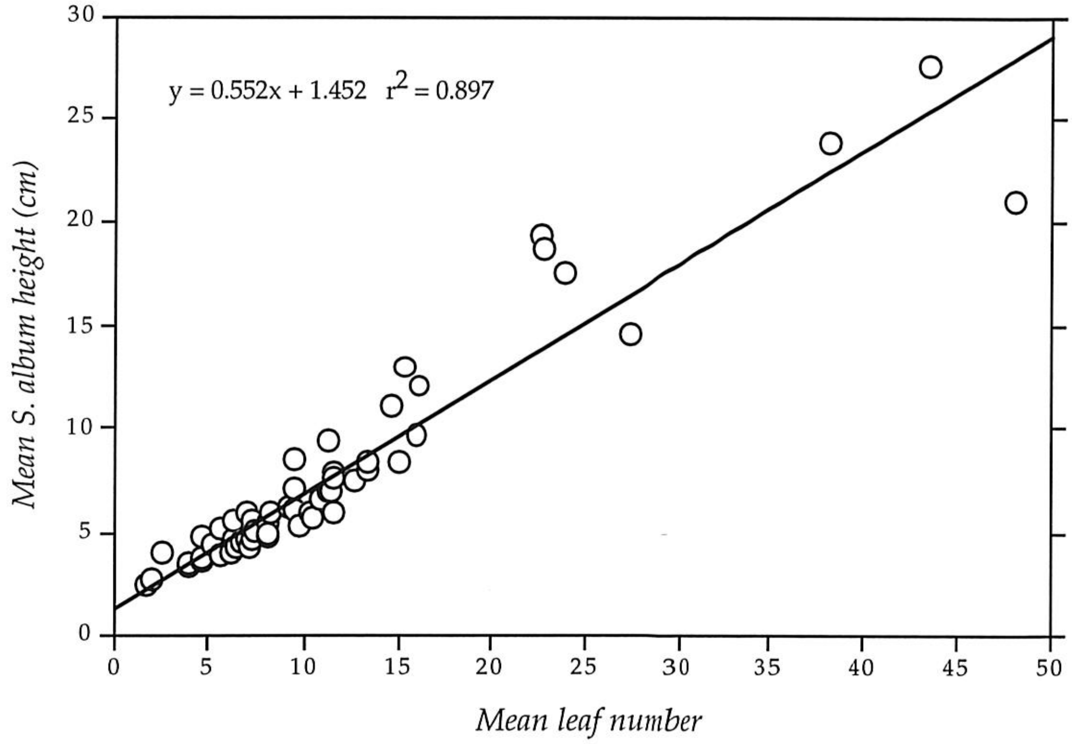


Figure 4. The relationship between mean height and leaf number of *S. album* over the trial for all seven treatments combined.

1.3 Harvest weights

Dry weight of *S. album* grown with no host (control) was poorest but not different from the three treatments with only one host each (Table 14, Appendix 6). Treatments with both *Alternanthera* sp. and *Citrus* rootstock (6 and 7) had heaviest *S. album* plants. Percentage moisture in control was highest while treatment 6 was least, however the range in % moisture was not great.

Table 14. Means of wet weight, dry weight and moisture content of *S. album* (Treatment numbers as in Table 10).

Treatment	n	Mean wet weight	Mean dry weight	Moisture (Wet-dry weight)	% **Moisture**
1	10	0.460c	0.087c	0.373c	81.09
2	10	1.920c	0.436c	1.439c	74.95
3	10	0.580c	0.118c	0.462c	79.65
4	10	2.040c	0.607c	1.433c	70.24
5	10	7.640b	2.170b	5.370b	70.29
6	10	15.070a	4.590a	10.480a	69.54
7	10	14.800a	4.360a	10.440a	70.54
F		10.16	9.20	10.44	
P		0.000***	0.000***	0.000***	

Means with the same letters in a column are not significantly different (Tukey test at the 0.05 level).

1.4 Haustoria development

There were significant differences in mean total number of haustoria observed at harvest. Plants with *Alternanthera* sp. and *Citrus* rootstock had most haustoria (Table 15, Appendix 7). Although control plants had few haustoria, this demonstrates that mechanical stimulation (i.e. hosts are not essential for haustoria) can cause formation of haustoria.

Table 15. Mean total numbers of haustoria of *S. album* by treatment (Treatments as in Table 10).

Treatment	N	Mean total number of haustoria
1	10	3.00 d
2	10	19.70 c
3	10	7.90 dc
4	10	12.80 cd
5	10	46.60 b
6	10	63.50 a
7	10	59.40 a
F		**55.87**
P		**0.000**

Treatments with the same letter do not differ using the Tukey test (p=0.05).

The combinations of hosts with *Alternanthera* sp. + *Citrus* rootstock (Treatment 6); and *Alternanthera* sp. + *A. acuminata* + *Citrus* rootstock (Treatment 7) stimulated haustoria better than single host treatments and the control. The greatest number of haustoria were found when *S. album* was with growing two hosts. It appears that there is little benefit from *A. acuminata* when it is the single host (Treatment 3). *Alternanthera* sp. as a single host (Treatment 2) was associated with six times as many haustoria as control plants.

2. *Alternanthera* sp.

2.1 Height.

Alternanthera sp. is a semi-prostrate bedding plant. During the course of the experiment, mean height increased gradually in all host combinations from 4-8 cm at the start to 14-18 cm at the finish. Plants grown alone did not become taller than those with *S. album* seedlings suggesting that *S. album* did not effect a decrease in height of *Alternanthera* sp. (Table 16, Figure 5, and Appendix 8).

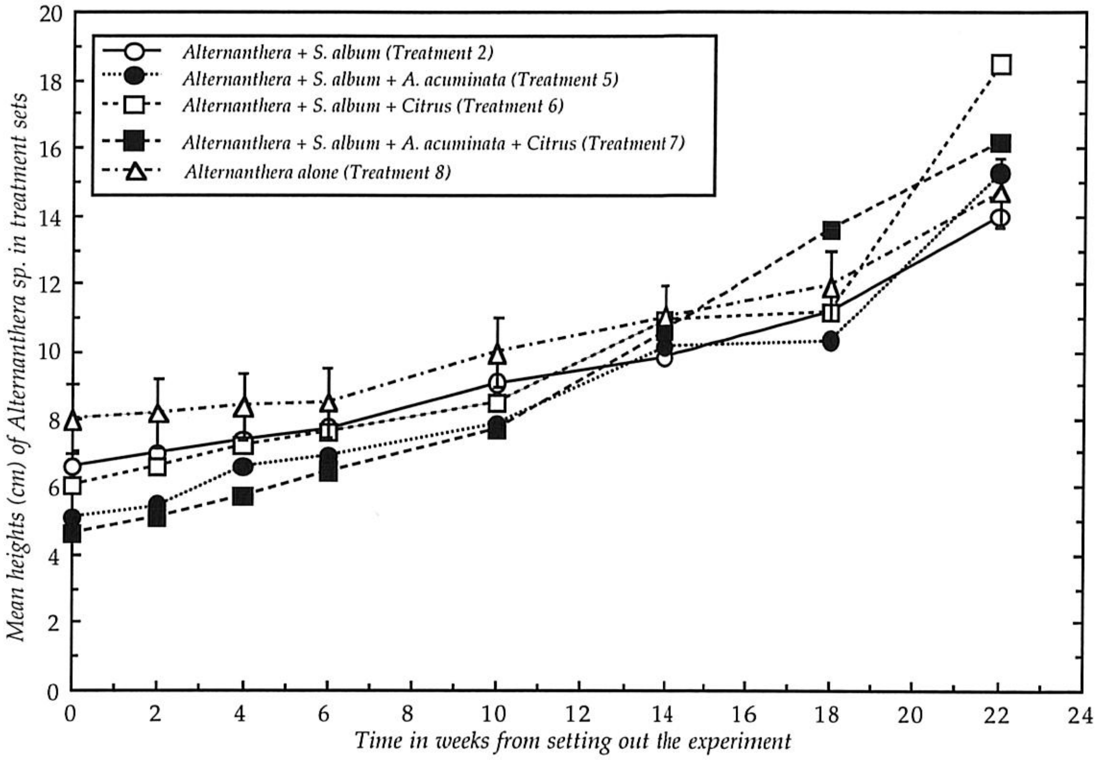


Figure 5. Height development of 5 treatments of *Alternanthera* sp. over the trial.

Table 16. Mean height of *Alternanthera* sp in 5 treatments by measurement times over the trial (Treatments as in Figure 5).

Treatment (n=15)	0 weeks	2 weeks	4 weeks	6 weeks	10 weeks	14 weeks	18 weeks	22 weeks
2	6.59 b	6.94 b	7.32 b	7.75 ab	9.04 b	9.79 b	11.12 bc	14.05 d
5	5.07 cd	5.44 c	6.55 bc	6.90 bc	7.85 bc	10.13 b	10.31 c	15.23 bc
6	6.01 bc	6.57 b	7.23 b	7.62 ab	8.48 bc	10.91 a	11.16 bc	18.46 a
7	4.59 d	5.07 c	5.70 c	6.45 c	7.69 c	10.57 ab	13.55 a	16.17 b
8	7.96 a	8.17 a	8.33 a	8.48 a	9.95 a	10.99 a	11.91 b	14.67 cd
F	**9.66**	**8.63**	**5.32**	**3.78**	**7.91**	**2.03**	**8.80**	**12.07**
P	**0.000** ***	**0.000** ***	**0.001** ***	**0.008****	**0.000** ***	**0.099** NS	**0.000** ***	**0.000** ***

Mean heights with the same letter in a column do not differ using the Tukey test (p=0.05).

However, *Alternanthera* sp. was able to grow taller where *S. album* had two or three hosts (Table 16). The tallest mean height of *Alternanthera* sp. at the end of the trial came from treatment 6 where *S. album* grew in association with *Alternanthera* sp. and *Citrus* rootstock.

2.2 Total leaf number

Mean total leaf numbers of *Alternanthera* sp. increased steadily over the trial (Figure 6). Total leaf number at the end of the trial was greatest when *Alternanthera* sp. was grown alone or as the only host to *S. album* (Treatments 2 and 8) (Table 17, Appendix 9). However, final leaf number ranks are very similar to starting leaf number ranks, suggesting that neither parasitism nor competition had much effect on growth of *Alternanthera* sp. as measured by leaf number.

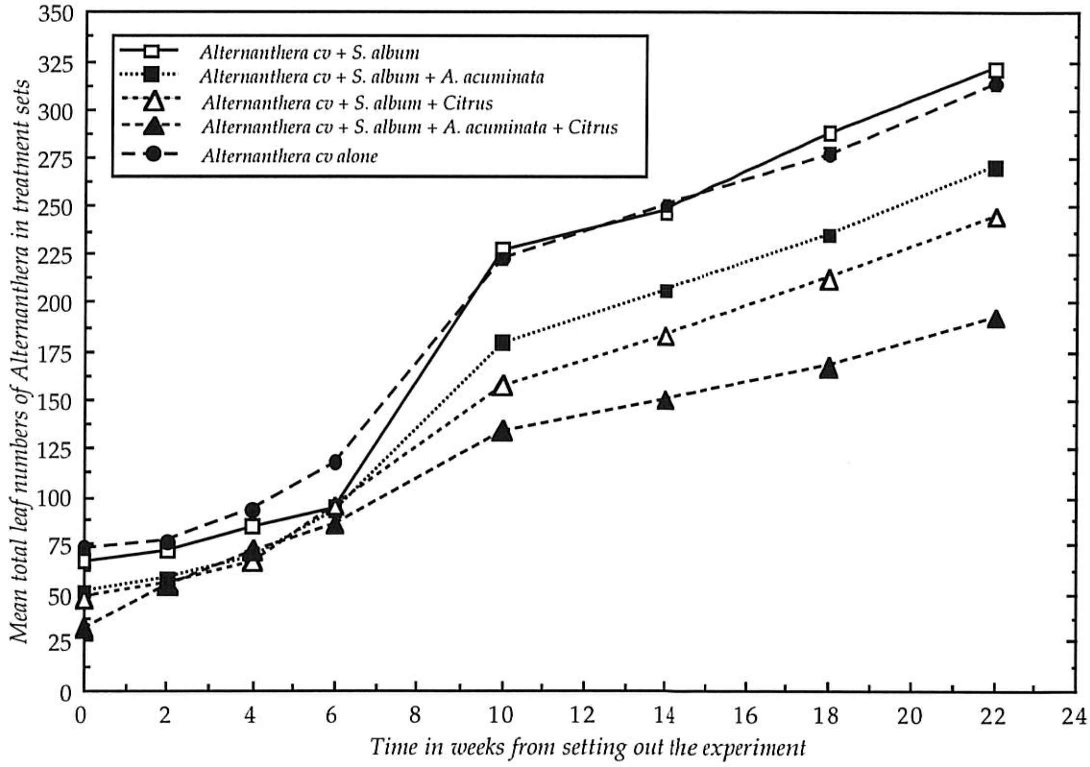


Figure 6. Mean total leaf number of *Alternanthera* sp. in 5 treatments over the trial.

Table 17. Mean total leaf numbers of 5 treatments of *Alternanthera* sp. over the trial (Treatments as in Figure 6).

Treatment (n=15)	0 weeks	2 weeks	4 weeks	6 weeks	10 weeks	14 weeks	18 weeks	22 weeks
2	66.27a	72.07a	83.73b	94.67b	227.33a	246.60a	288.33a	321.13a
5	50.80b	58.13b	68.20c	92.47bc	179.20b	205.53b	235.27b	269.87b
6	47.80b	55.80b	66.93c	94.80b	156.73c	182.33c	212.87c	244.33c
7	32.60c	53.87b	71.73c	85.80c	133.93d	149.33d	167.80d	192.67d
8	73.07a	76.87a	92.53a	117.33a	222.87a	250.53a	277.13a	314.00a
F	26.40	11.11	9.94	11.51	40.05	51.86	51.69	100.01
P	0.000 ***	0.000 ***	0.000 ***	0.000 ***	0.000 ***	0.000 ***	0.000 ***	0.000 ***

Means with the same letter in columns do not differ using the Tukey test (p=0.05).

2.3 Harvest weights

Dry weight of *Alternanthera* sp. with *S. album* (Treatment 2) was not less than when it was grown alone (Treatment 8) or in combination with *A. acuminata* (Treatment 5) (Table 18, Appendix 10). These three treatments had significantly greater mean dry weight of *Alternanthera* sp. than the combinations with *Citrus* rootstock (Treatments 6 and 7). This suggests *Citrus* rootstock had a competitive effect on *Alternanthera* sp.

Table 18. Means of wet weight, dry weight and moisture content of *Alternanthera* sp. in 5 treatments (Treatments as in Figure 6).

Treatment	n	Mean wet weight	Mean dry weight	Moisture	% Moisture
2	10	170.23 a	45.120 a	125.11 a	73.49
5	10	162.55 a	44.770 a	117.78 a	72.46
6	10	123.81 b	31.410 b	92.40 b	74.63
7	10	109.47 b	29.920 b	80.47 b	73.51
8	10	154.32 a	43.670 a	110.65 a	71.70
F		8.65	12.25	7.21	
P		0.000 ***	0.000 ***	0.000 ***	

Means with the same letter in columns do not differ using the Tukey test (p=0.05)

3. *Acacia acuminata*

3.1 Height

A. acuminata grew poorly in this experiment (Figure 7). Mean heights in all four treatments changed very slowly until 14 weeks. *A. acuminata* alone (Treatment 9) was consistently taller until 18 weeks. From 18 weeks *A. acuminata* as a sole host (Treatment 3) increased dramatically in height.

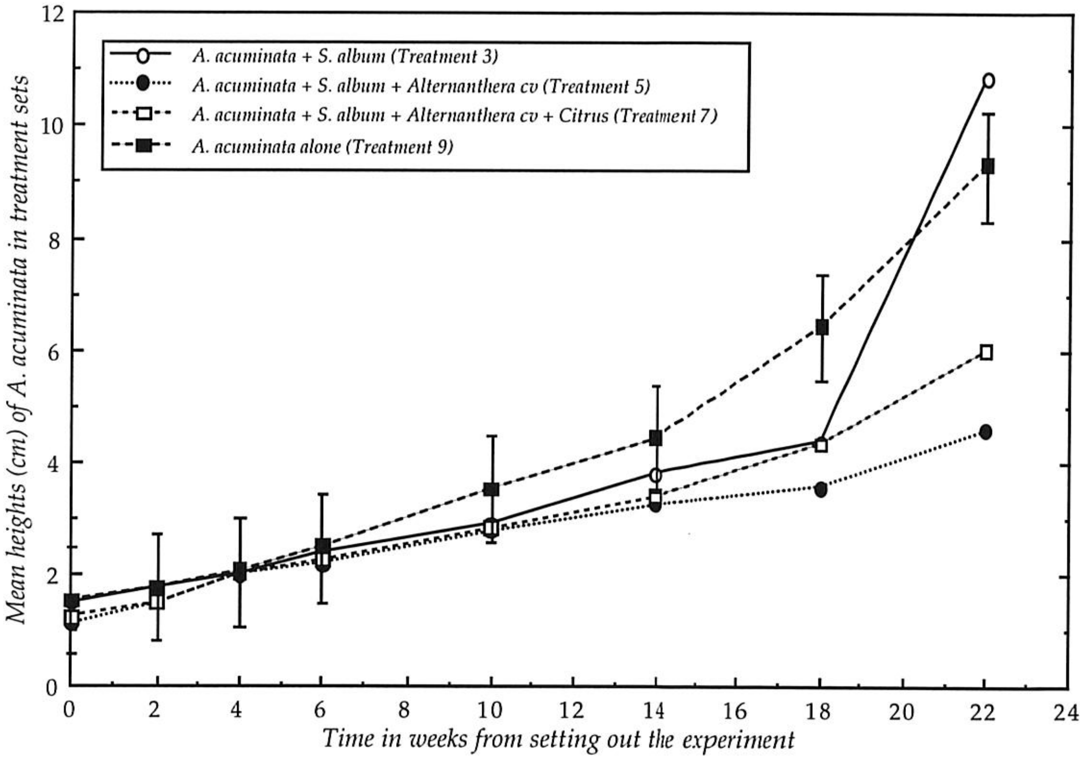


Figure 7. Height development of *A. acuminata* in 4 treatments over the trial (Error bars are standard deviation).

Analysis of variance revealed significant differences in height of *A. acuminata* between treatments at the start and finish (Table 19, Appendix 11). Between 4 and 18 weeks there were no significant differences in height between treatments. Tallest mean height at the end of the trial came from *A. acuminata* with *S. album* (Treatment 3), but this was not significantly different from *A. acuminata* alone (Treatment 9).

Table 19. Mean height of *A. acuminata* in 4 treatments over the trial (Treatments as in Figure 7).

Treatment (n=15)	0 weeks	2 weeks	4 weeks	6 weeks	10 weeks	14 weeks	18 weeks	22 weeks
3	1.49 a	1.75 a	1.97	2.39	2.89	3.79	4.37	10.85 a
5	1.10 b	1.51 b	1.99	2.19	2.75	3.26	3.55	4.49 b
7	1.22 b	1.51 b	2.02	2.26	2.82	3.41	4.33	6.00 b
9	1.54 a	1.77 a	2.05	2.47	3.52	4.43	6.43	9.31 ab
F	7.89	2.59	0.07	0.46	0.76	0.48	0.96	1.46
P	0.00	0.06	0.98	0.71	0.52	0.70	0.42	0.24
	***	NS	NS	NS	NS	NS	NS	NS

Means with the same letter in a column do not differ using the Tukey test (p=0.05).

3.2 Total phyllode number

Mean phyllode numbers were 4-6 only for the first 6 weeks and generally, phyllode number of *A. acuminata* increased slowly over the trial (Figure 8). *A. acuminata* with *S. album* (Treatment 3) produced dramatically more phyllodes after 18 weeks.

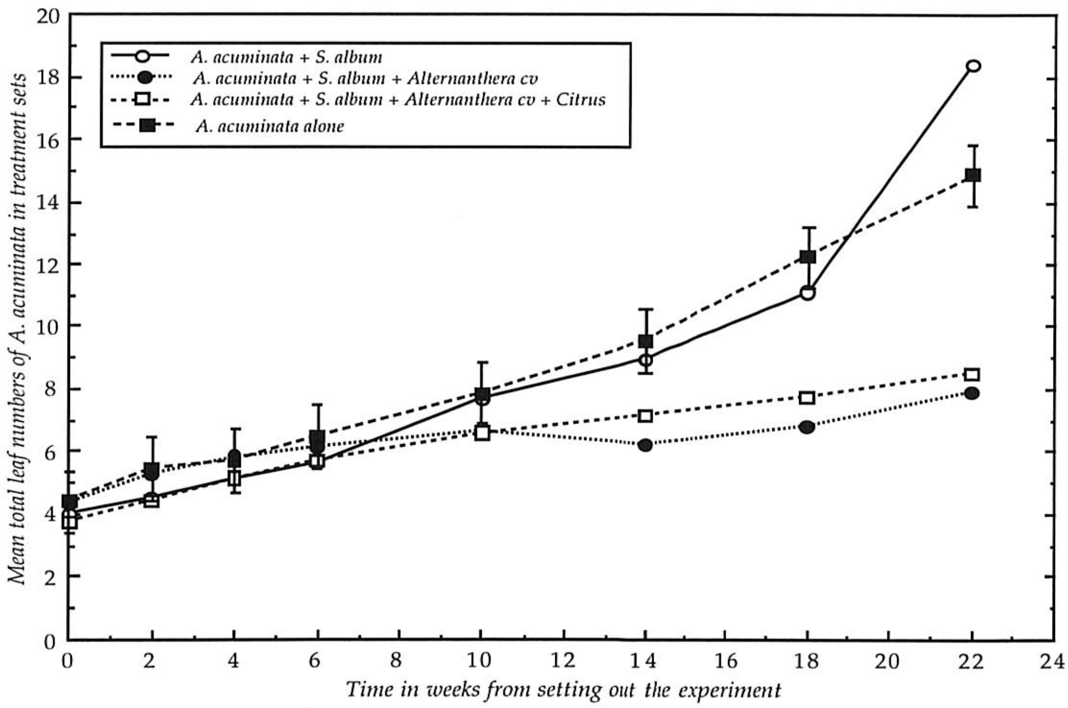


Figure 8. Mean total phyllode number of 4 treatments with *A. acuminata* over the trial (Treatments as in Figure 7). Error bars are standard deviation.

Analysis of variance showed that mean phyllode numbers only differed at 2 weeks. Numbers at setting out differed slightly. The Tukey test suggests that phyllode numbers at the finish were greater with *A. acuminata* as the sole host (Table 20, Appendix 12).

Table 20. Mean total leaf number of 4 treatments of *A. acuminata* over the trial (Treatments as in Figure 8).

Treatment (n=15)	0 weeks	2 weeks	4 weeks	6 weeks	10 weeks	14 weeks	18 weeks	22 weeks
3	4.00 ab	4.53 b	5.07	5.60 b	7.67	8.93	11.07	18.40 a
5	4.33 a	5.27 a	5.80	6.13 ab	6.67	6.20	6.80	7.87 b
7	3.73 b	4.40 b	5.13	5.73 ab	6.60	7.13	7.73	8.53 ab
9	4.40 a	5.47 a	5.73	6.47 a	7.87	9.53	12.20	14.87ab
F	**2.70**	**5.11**	**1.80**	**1.42**	**0.65**	**1.23**	**1.29**	**1.78**
P	**0.054** NS	**0.003** **	**0.159** NS	**0.247** NS	**0.587** NS	**0.309** NS	**0.286** NS	**0.161** NS

Means with the same letter in a column do not differ using the Tukey test (p=0.05).

3.3 Harvest weights

Comparison of mean dry weights of *A. acuminata* from the four treatments revealed significant differences among treatments. Treatment 7 (*A. acuminata* associated with *S. album*, *Alternanthera* sp. and *Citrus* rootstock) produced significantly more dry weight than the other 3 treatments (Table 21, Appendix 13). These plants were also considerably less hydrated (55% moisture) than the others.

Table 21. Mean of wet weight, dry weight and moisture content of *A. acuminata*.

Treatment	N	Mean wet weight	Mean dry weight (Biomass)	Moisture	% Moisture
3	10	2.120 b	0.6100 b	1.5100 b	71.23
5	10	0.330 c	0.0630 c	0.2670 c	80.91
7	10	5.340 a	2.3700 a	2.9700 a	55.62
9	10	0.990 c	0.2730 c	0.7170 c	72.42
F		42.37	99.14	24.54	
P		0.000***	0.000***	0.000***	

Means with the same letter in a column do not differ using the Tukey test (p=0.05).

4. *Citrus* rootstock

4.1 Height

The pattern of mean height of *Citrus* rootstock between treatments remained the same over the trial (Figure 9). Plants increased steadily from 12-20 cm at the start to 50-80 cm at the end (Figure 9).

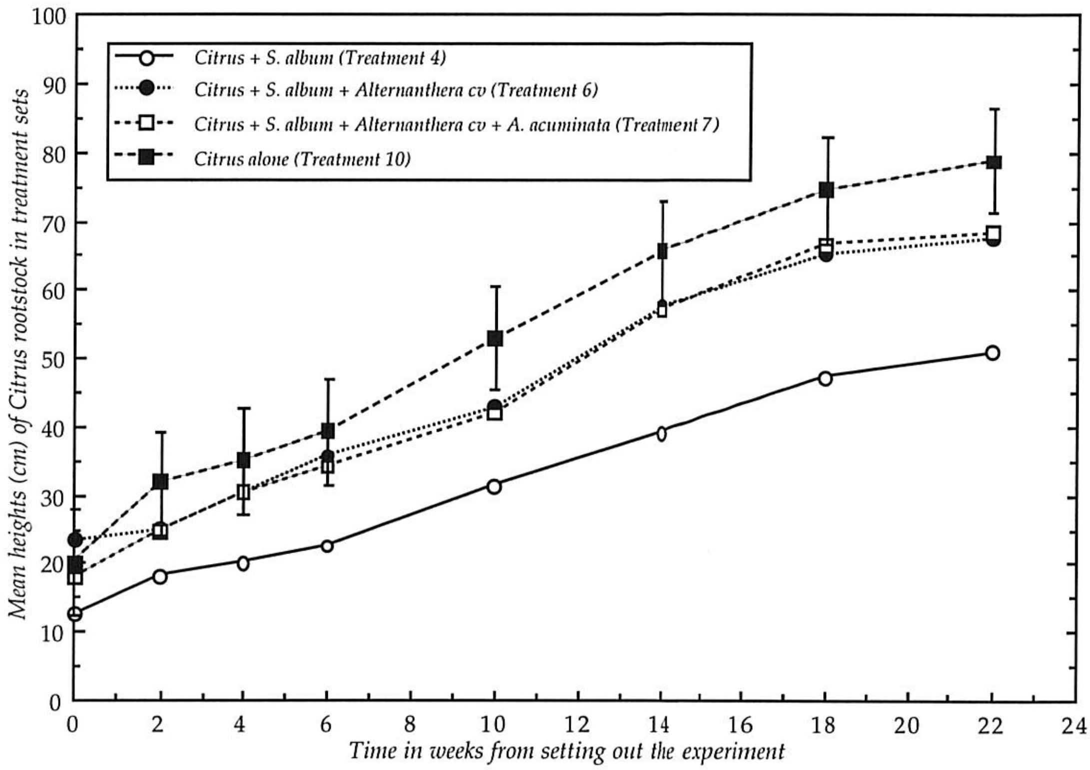


Figure 9. Height development of 4 treatments of *Citrus* rootstock over the trial (Error bars are standard deviation).

This initial difference in height between treatments may have influenced the continuing difference over the trial so that it is not possible to say whether height is definitely reduced by *S. album*. However, after 22 weeks *Citrus* rootstock alone was tallest and these plants had grown most over the period (58.81 cm) (Table 22, Appendix 14). *Citrus* rootstock as the single host (Treatment 4) was shortest and had grown least (38.66 cm). *Citrus* rootstock in combination with *S. album* and one or two hosts was intermediate in height with these sets having grown about 51 cm each.

Table 22. Mean heights of *Citrus* rootstock in 4 treatments over the trial from potting until 22 weeks (Treatments as in Figure 9).

Treatment (n=15)	0 weeks	2 weeks	4 weeks	6 weeks	10 weeks	14 weeks	18 weeks	22 weeks
4	12.43 c	18.09 c	20.11 c	22.35 c	31.13 c	39.09 c	47.23 c	51.09 c
6	16.87 b	24.97 b	30.20 b	35.57 ab	42.67 b	57.59 b	65.34 b	67.56 b
7	17.70 b	24.77 b	30.25 b	33.95 b	41.88 b	57.07 b	66.51 b	68.55 b
10	20.03 a	31.83 a	34.93 a	39.23 a	52.88 a	65.49 a	74.65 a	78.84 a
F	**16.63**	**15.33**	**13.72**	**14.39**	**12.37**	**16.18**	**13.16**	**12.70**
P	0.000 ***	0.000 ***	0.000 ***	0.000 ***	0.000 ***	0.000 ***	0.000 ***	0.000 ***

Means with the same letter in a column do not differ using the Tukey test (p=0.05).

4.2 Total leaf number

Leaf number of *Citrus* rootstock in the four treatments increased at about the same rate for each set over the trial (Figure 10). The pattern was a gradual increase until 6 weeks, followed by a dramatic increase to 22 weeks with *S. album* alone or with *Alternanthera* sp. (Treatment 4 and 6). With all 3 hosts (Treatment 7), leaf number increased slightly until 2 weeks, steadily increased to 6 weeks and increased dramatically to 22 weeks. *Citrus* rootstock alone (Treatment 10), exhibited a steady increase throughout.

Analysis of variance suggests that treatment sets showed significant differences for the first 6 weeks. There were then no significant differences between treatments after 6 weeks until the end of the trial (Table 23, Appendix 15). At the end of the trial, mean total leaf number of *Citrus* rootstock as sole host (Treatment 4) was greatest but not significantly different from the *Alternanthera* sp. and *S. album* combination (Treatment 6). *Citrus* rootstock alone (Treatment 10) had lowest mean total leaf number but this did not differ from 3 other sets. By the end of the trial, total leaf number had increased by 10 times when grown as the sole host (Treatment 4) and five times when in combination with *Alternanthera* sp. and *S. album* (Treatment 6)

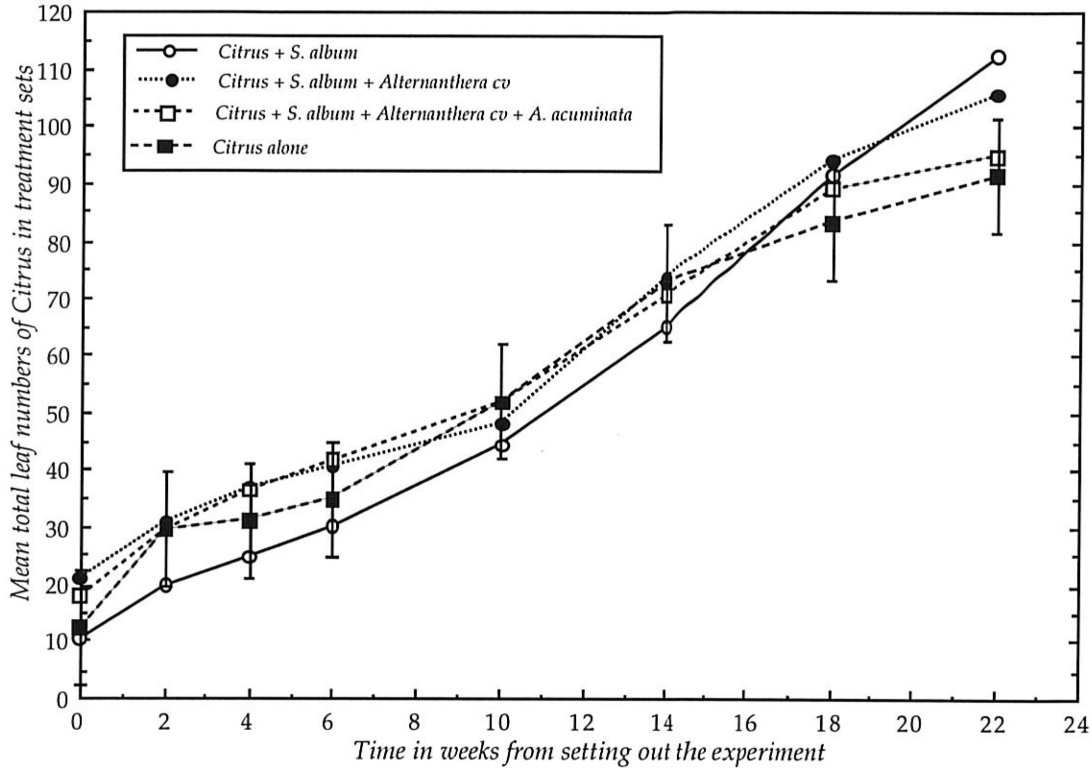


Figure 10. Increase in total leaf number of 4 treatments of *Citrus* rootstock over the trial from potting until 22 weeks (Error bars are standard deviation).

Table 23. Mean total leaf numbers of *Citrus* rootstock in 4 treatments over the trial from potting until 22 weeks (Treatments as in Figure 10).

Treatment (n=15)	0 weeks	2 weeks	4 weeks	6 weeks	10 weeks	14 weeks	18 weeks	22 weeks
4	10.40 b	19.73 c	24.87 b	29.87 b	44.40 a	64.73 a	91.40 a	112.47 a
6	21.13 a	30.67 a	36.93 a	40.67 a	48.00 a	73.47 a	94.20 a	105.67 ab
7	17.93 a	29.60 b	36.20 a	41.47 a	51.67 a	70.60 a	89.27 a	94.80 b
10	12.53 ab	29.67 b	31.27 ab	34.80 ab	51.93 a	72.73 a	83.27 a	91.33 b
F	4.55	4.88	4.83	4.10	1.13	0.61	0.61	2.43
P	0.006**	0.004**	0.005**	0.011*	0.346NS	0.611NS	0.610NS	0.074NS

Means with the same letter in columns do not differ using the Tukey test (p=0.05).

4.3 Harvest weights

Comparison of mean dry weight of *Citrus* rootstock from the 4 treatments reveal a significant difference between treatments (Table 24, Appendix 16). Greatest dry weight came from the treatment with only *Citrus* rootstock. Least weight came from treatment 4 where it was the sole host with *S. album*. The two other treatments were intermediate. It appears that the dry weight of *Citrus* rootstock when associated with *S. album* and other hosts, is significantly lighter than when *Citrus* rootstock is grown alone. Dry weight of *Citrus* rootstock is significantly reduced by parasitism, loss to parasitism may be mediated by presence of another host species.

Table 24. Mean wet weight, dry weight and moisture content of 4 treatments of *Citrus* rootstock.

Treatment	n	Mean wet weight	Mean dry weight/biomass	Moisture	% Moisture
4	10	35.95 c	16.16 c	19.79 c	55.05
6	10	45.33 b	20.10 b	25.23 b	55.66
7	10	46.10 b	22.44 b	23.66 bc	51.32
10	10	59.43 a	27.35 a	32.08 a	53.98
F		13.19	18.70	9.66	-
P		0.000 ***	0.000 ***	0.000 ***	

Means with the same letter in columns do not differ using the Tukey test (p=0.05).

Discussion

Cultivation of *S. album* is more complicated than cultivation of monoculture plantations, due to the need for provision of a range of hosts. It is widely accepted that the nursery stage requires that a pot-host is present (Srinivasan *et al.* 1992; Surata 1992; Nasi 1995; Fox *et al.* 1996; Radomiljac 1998). *Alternanthera nana* is a superior pot-host for *S. album*, and can directly affect survival and growth of *S. album* in the field (Radomiljac 1998). There appear to be no previous studies of multiple pot hosts at the nursery stage reported in the literature.

In this trial, *S. album* grown with *Alternanthera* sp. were taller and heavier than when grown without *Alternanthera* sp. The four *Alternanthera* sp. were best in terms of mean height between age 10 and 22 weeks. *S. album* seedlings can initiate haustoria development within 30 days after planting with hosts (Nagaveni and Srimarthi 1985). My results suggest that the parasitic association between *S. album* and hosts started at 28 days after seedlings were placed together with hosts. Mean heights of *S. album* in four treatments with *Alternanthera* sp. at 22 weeks were 19–28 cm. This experiment was shorter than the 26 weeks used to obtain *S. album* heights of > 25 cm when associated with *Alternanthera* cv., and the legumes *Crotalaria juncea, Desmanthus virgatus, Cajanus cajan* and *Sesbania grandiflora* in Timor (Fox *et al.* 1995 b).

The length of time that *S. album* and its pot host are housed in the nursery prior to field planting affects the economics of nursery and plantation management. Fox *et al.* (1995 b) suggest that *S. album* seedlings should be > 25 cm tall at planting time to maximise survival. In Timor, 26 weeks is adequate, providing one of several superior pot hosts (including *Alternanthera* cv) is used in companion planting from about the time of sandalwood germination. Radomiljac and McComb (1998) investigated duration time after insertion of *Alternanthera nana* into pots containing only *S. album.* Periods of 109-134 days of association in the nursery stage increased subsquent survival in the field.

For convenience I germinated *S. album* separately, prior to potting of host and parasite together. In commercial applications it may be more appropriate to sow directly into pots and then sow the host to be used, or insert cuttings in the case of *Alternanthera* sp. Pot hosts may be utilised for periods longer than 134 days in India and Indonesia (Srinivasan *et al.* 1992; Surata, Harisetijono and Sinaga 995; Fox *et al.* 1996). In the present trial it is clear that *Alternanthera* sp. was a superior pot host, as it stimulated *S. album* more effectively than the other hosts used. A balance between benefit to the *S. album* and competition effects requires that pot size must be adequate for the nursery duration and that excess *Alternanthera* sp. material be removed by pruning if the sandalwood appears to be suffering from competition.

Leaf number increased dramatically between 18 and 22 weeks. At the end of the trial, the four treatments with *Alternanthera* sp. had significantly more foliage than those without *Alternanthera* sp. and the control. Leaf number of *S. album* slightly decreased at 14 to 18 weeks with no host. This may have resulted from a lack of certain nutrients (Struthers *et al.* 1986) in the pot medium, or absence of haustorial attachments to provide resources (Barrett and Fox 1994), as both appear to be associated with increased leaf fall. *S. album* is a partial root parasite and partial phytoautotroph (Iyengar 1965). Commonly, parasitic plants are smaller than hosts, such as the herbaceous root parasite *Rhinanthus serotinus* Schonh. (Klaren and Jansen 1978), and depend on hosts for mineral nutrition. On the other hand, *S. album* can be a relatively large tree in its habit. This implies that not all nutrients are transferred from hosts, but some nutrients are absorbed directly from the soil through the sandalwood root system (Sreenivasa Rao 1933; Iyengar 1960; Srinivasan *et al.* 1992), because *S. album* roots possess cation exchange, comparable to normal plants, and *S. album* has an ability to absorb nutrients from the soil (Parthasarathi, Gupta and Rao 1974). However, as a hemi-parasite, *S. album* seedlings depend, at least to some extent, on hosts for mineral nutrition (Fox *et al.* 1995 b).

Significant relationships were found between mean leaf number and mean height of *S. album*. Leaf number increases linearly with height until the height reaches about 27 cm. Seedlings taller than this had a more rapid increase in leaf number. This suggests that a critical stage of adequate haustorial attachment had been attained and this was related to both attained size and the presence of a suitable host in *Alternanthera* sp. It is of interest that *Alternanthera* sp. plants did not become taller when grown alone than when grown with *S. album* seedlings, *A. acuminata* and *Citrus* rootstock. The highest mean total leaf number occurred with *Alternanthera* sp. grown with *S. album*, at the end of the trial.

A. acuminata grew poorly in all combinations. This may have been more to do with pot conditions being unsuitable rather than parasitism *per se*. *A. acuminata* is not suitable as a small "in pot" host for *S. album* whereas it may be a suitable large tree host for established sandalwood plants. This *Acacia* has a number of useful properties including drought and frost tolerance (Barrett 1995).

Citrus rootstock plants grew well with *S. album*, but less well when associated with other hosts. Growth was poor when associated with *S. album* only, suggesting that it was effectively parasitised and suffered as a consequence. On the other hand, this experiment showed that *S. album* growth is poorer in the nursery stage when associated with the combination of *A. acuminata* and *Citrus* rootstock. Slow growth of *A. acuminata* suggests it required different conditions or that it grew poorly in competition with *S. album*. *S. album* differentially parasitises *Citrus* rootstock and *A. acuminata*, and is best when grown with *Alternanthera* sp. as it was taller than without *Alternanthera* sp. and also produced greater dry weight.

It is possible that sandalwood grows poorly in relatively nutrient poor sites (Mathies 1995). Greatest dry weight of *S. album* was obtained with combinations of *Alternanthera* sp. + *Citrus* rootstock as hosts while in the absence of any hosts weight was lightest. *S. album* seedlings are able to survive in the absence of a pot-host when conditions are favourable.

Legumes are not necessarily better pot hosts than non-legumes (Radomiljac 1998). Dry weight of *Citrus* rootstock when associated with *S. album* was least. Watkinson and Gibson (1988) note that the balance between parasite and host is seen in growth. Poor growth of hosts indicates that the parasite damages the host. This suggests that *S. album* draws nutrients from *Citrus* rootstock, but benefited more when associated with several hosts.

There were significant differences in haustoria development associated with *S. album*. Combinations of hosts had more haustoria than single hosts, while the control set had only a few haustoria. Parasitic species including *S. album* (Rama Rao 1911); *Nuytsia floribunda* (Labill.)R.Br. (Loranthaceae) (Herbert 1919); and *Olax phyllanthi* (Labill.) R.Br. (Olacaceae) (Pate, Kuo and Davidson 1990) tend to be catholic in the range of host species. Haustoria attachment appears dependent on the availability of potential host roots. In this experiment the best haustoria development came with the combination of *Alternanthera* sp. and *Citrus* rootstock.

Plant parasites can attack and use multiple hosts simultaneously for their nutrients (Musselman and Mann 1978, Gibson and Watkinson 1989). Hosts that cause better parasite performance may suffer more from parasitism and there will be some upper limit to the amount of parasitism that can be tolerated by particular hosts. Increased growth and vigour shown after seedling-host connections are made is associated with prior lack of nutrient uptake by the parasite. At the seedling stage, cotyledonary nutrient resources are adequate for the young seedling and the rate at which these become inadequate will depend on the rate of seedling growth. Seedlings that lose leaves or decline in height may be showing the first signs of nutrient limitation associated with exhaustion of cotyledons and lack of, or poor, haustorial attachment.

Seedlings benefit not only from nutrients transferred, but in the field they also benefit from shelter and shade that hosts provide (Barrett and Fox 1994). Hosts are beneficial for up to three years at least, in terms of *S. album* survival, height, leaf number, dry weight, and chlorophyll production. After making host attachments, seedlings add new foliage and are more robust. In the field, host preferences of epiphytic parasites can be observed directly, those of root parasitic trees can only be inferred without exploring root connections (Pennings and Callaway 1996). Pot trials, which contain paired plants of host and parasite, have been used to show direct negative effects on host growth (Marvier 1996). Growth is clearly enhanced when associated with some hosts (Rai 1990, Fox *et al.* 1996, Marvier 1996). The combination of the 2 hosts *Alternanthera sp.* and *Citrus* rootstock allowed *S. album* to grow relatively rapidly in height and total mass. This suggests that there may be considerable benefit in provision of multiple hosts in the nursery.

Conclusion

S. album seedling height increased linearly to 28 cm after 22 weeks (154 days) when grown with a combination of the 2 hosts *Alternanthera* sp. and *Citrus* rootstock. *Alternanthera* sp. as a single pot-host promotes *S. album* growth better than *A. acuminata* and *Citrus* rootstock. Height, leaf number and haustoria development were superior with *Alternanthera* sp. as the pot-host.

Unhosted *S. album* can survive without a host for 22 weeks but in this state growth is poor. This experiment also indicated that hosts affect growth rate of *S. album* by as soon as 28 days after planting with hosts. Comparison of dry weights of plants indicates that *S. album* diminishes hosts.

The experiment suggests that combinations of *Alternanthera* sp. and *Citrus* rootstock give greater contributions to growth rate of *S. album*, in terms of height, haustoria development and dry weight than a single host. Multiple hosting of *S. album* at the seedling stage has not been reported earlier.

5. Growth of Hosted and Unhosted *S. album* with Plant Nutrients Supplied

Introduction

The extent of dependence of parasitic plants on host plants and the degree of parasitism are variable. Some parasites lack chlorophyll (e.g. *Orobanche*) and are totally parasitic. Mistletoes lack roots and draw all essential nutrients from the host. *S. album*, as a hemi-parasitic tree species possesses functional amounts of chlorophyll, but still requires certain nutrients and water from host plants (Sreenivasa Rao 1933, Iyengar 1960, Srinivasan *et al.* 1992). Presumably it is unable to acquire sufficient directly for itself, although *S. album* roots possess cation exchange capacity, comparable to normal plants (Parthasarathi *et al.* 1974). It is known that *S. album* can draw moisture from the host, and some nutrients. The following are reported: N, P (Iyengar 1960); P, K, Mg (Rangaswamy, Jain and Parthasarathi 1986); Ca and Fe (Sreenivasa Rao 1933); K, Ca, Mg, Fe, Cu, and Zn (Ramaiah, Parthasarathi and Rao 1962). Amino acids may be transferred from the host (Struthers *et al.* 1986). *Santalum* seedlings can survive for up to a year in the absence of a host (Rama Rao 1911, Wijesuriya and Fox 1985, Widiarti 1989). During the period of pre-parasitism it must depend on cotyledonary nutrients and some nutrients from the growing medium or soil. Other research suggests that some un-hosted *S. album* seedlings can survive between 2 to 3 years, but are in poor health (Nagaveni and Srimathi 1985). The Western Australian sandalwood (*S. spicatum*) can survive up to 2 years without host plants, as long as the endosperm provides nutrition, but many will remain in poor health thereafter, even when hosts are supplied (Loneragan 1990).

At the nursery stage nutrient resources are provided by seed reserves and from the soil. As seed reserves are exhausted, haustorial attachment to the host seedlings becomes critical for survival (Fox *et al.* 1995 b). About 70% of *S. album* seedlings are found in association with potential hosts and will develop haustoria within 30 days after germination. Up to 90% do so within one year (Nagaveni and Srimathi 1985). Mortality of *S. album* seedlings occurs when roots do not develop haustorial attachments within about one year. This condition may be due to an inability to obtain an element for which the host is an essential nutrient source, or the requirement for sufficient nutrients to maintain growth after exhaustion of the cotyledons. The presence of the haustorial attachment at an early stage is essential for longer-term survival.

In larger plants of *S. album*, inadequate nutrition is associated with increased leaf fall and premature fruit fall. *S. album* seedlings without supplementary Ca in nutrient omission trials fail to grow at all in the absence of hosts. About the same proportion of some nutrients (Ca, Fe, N) and up to > 50% (K) were found in the parasitic mistletoe, *Amyema preissii*, when associated with the host *A. acuminata*, and high K/Ca ratios are a feature of attached angiosperm hemi-parasites (Lamont and Southall 1982, Lamont 1983). Available evidence indicates differences in nutrients obtained by parasitic species from hosts and different nutrients are provided by different hosts (Pate, True and Rasins 1991). It is likely many seedlings may not survive, indirectly, through deficiencies. Preferential uptake of the more mobile ions in both *S. album* and *S. spicatum* suggest there are similarities between different *Santalum* species whether they are hosted or not. Variation in nutrient content of pre-parasitic seedling *S. spicatum* foliage may reflect variable fruit load as seedlings differ in growth between ecotypes and nutrient concentrations decline with *Santalum* growth. As seedlings become hosted, variation in nutrient content must reflect differing host contributions.

To establish healthy plantations it is necessary to recognise deficiencies, as symptoms may have similarities with the effects of fungal or virus disease. Lack of each of the major nutrient elements results in stunted growth, reduced leaf area and increased leaf thickness (Barrett, Fox and Suriamihardja 1993). Ca and Fe are critical in the nutrition of sandalwood. N deficiency leads to general chlorosis with reddening of leaf tips and margins, commencing on older leaves. With a lack of P, yellow blotches develop, initially on older leaves. These become yellow from the tips with some reddening of the distal end. K deficiency is manifested by yellow mottling and puckering interveinally with contrasting green veins (Barrett *et al.* 1993). Ca deficient plants retain green colour on older leaves with some purplish tinges. New leaves become progressively yellower, leaving only the mid-vein with some green. Fe deficient plants retain a deep green colour in older leaves, new leaves are interveinally and marginally chlorotic but chlorophyll level is not affected (Fox and Barrett 1995). Absence of trace elements (Cu, Zn, Mn, Mo) also stunts seedlings, which eventually die (Srinivasan *et al.* 1992).

The objective of growing *S. album* and *Alternanthera* sp. in a sterile medium was to determine the response of *S. album* seedlings to nutrient solute supplementation with one of 6 different treatment sets. These were: N, P, K; N, P, K + trace elements; Ca; Mg; Fe; and trace elements. Finally, a control set without any supplementary nutrient solutes was used. Nutrient solutes were provided by direct application to foliage of plants once per week for 20 weeks to each of three sets of plants (either *S. album* alone; *S. album* with *Alternanthera* sp.; or *Alternanthera* sp. alone), each replicates.

Results

The experimental results are presented in sections that describe growth of the two species: *S. album* and *Alternanthera* sp. by treatments. Plant heights are presented first and then number of leaves, plant roots, haustorial development and finally, harvest weight. Chemical nutrient analyses were not carried out, because of the limitation of available foliar dry weight of each treatment.

Plant heights and leaf numbers

In general, *S. album* associated with *Alternanthera* sp., grew slightly better than *S. album* grown alone in respect to nutrient treatment. *S. album* was in a condition of good health when associated with *Alternanthera* sp. in all sets. *Alternanthera* sp., both with *S. album* and alone, increased in height and leaf number when treated with N, P, K (*Alternanthera* sp. with *S. album*) or N, P, K + trace elements (*Alternanthera* sp. alone). Changes in mean height and leaf number over the trial are illustrated (Figures 11 and 12).

In the control sets, *S. album* grown alone was poor. Of the 4 seedlings in the set, only one grew well over the period of 20 weeks. Three other seedlings grew well initially: to 12 weeks (one seedling); or 15 weeks (2 seedlings). These then declined and dried back from the apices. Leaf numbers decreased at about 8 weeks (2 seedlings), 12 weeks (one seedling) and at 16 weeks (one seedling). *S. album* growing with

Alternanthera sp. in the control set, in general maintained good health condition over the trial. Only one seedling lost leaves at 12 weeks, but after that increased at 16 weeks until the end of the trial. *S. album* associated with *Alternanthera* sp. in the control set was significant taller in height than *S. album* alone.

Mean height and leaf number of *S. album* with and without *Alternanthera* sp. treated with N, P, K; or N, P, K and trace elements were similar. All seedlings survived except for 3 seedlings treated with N, P, K that died at 14 weeks, one in *S. album* alone and two seedlings in *S. album* with *Alternanthera* sp. Ca and Mg solutions affected plants similarly in terms of height and leaf number, in both *S. album* with and without *Alternanthera* sp. (Ca), but there was a significant difference in leaf number when treated with Mg. All seedlings in both sets survived over the trial. Two seedlings (treated with Mg) in the *S. album* alone set died at 12 weeks and one seedling with *Alternanthera* sp. died at 17 weeks. The treatment with Fe solution did not produce any significant differences in height or leaf number during the trial. However, trace elements appeared to stimulate height of *S. album* in both sets at the same rate. *S. album* with *Alternanthera* sp. had significantly greater leaf numbers at the end of the trial. All seedlings of *S. album* without a host grew poorest in this treatment.

Alternanthera sp. grown with *S. album* in control sets and in all treatments increased in height and leaf number at the same rate over the trial. *Alternanthera* sp. alone when treated with N, P, K was significantly tallest among other treatments and control sets. In association with *S. album*, there were significant differences in heights and leaf numbers when treated with N, P, K and trace elements. Some fungal infection was observed with *Alternanthera* sp. in the N, P, K treatment. Two *Alternanthera* sp. plants in association with *S. album* and treated with Ca solution were poorer in shoot development at 16 weeks and one seedling in *Alternanthera* sp. alone, treated with N, P, K was in poor health from 14 weeks until the end of the trial.

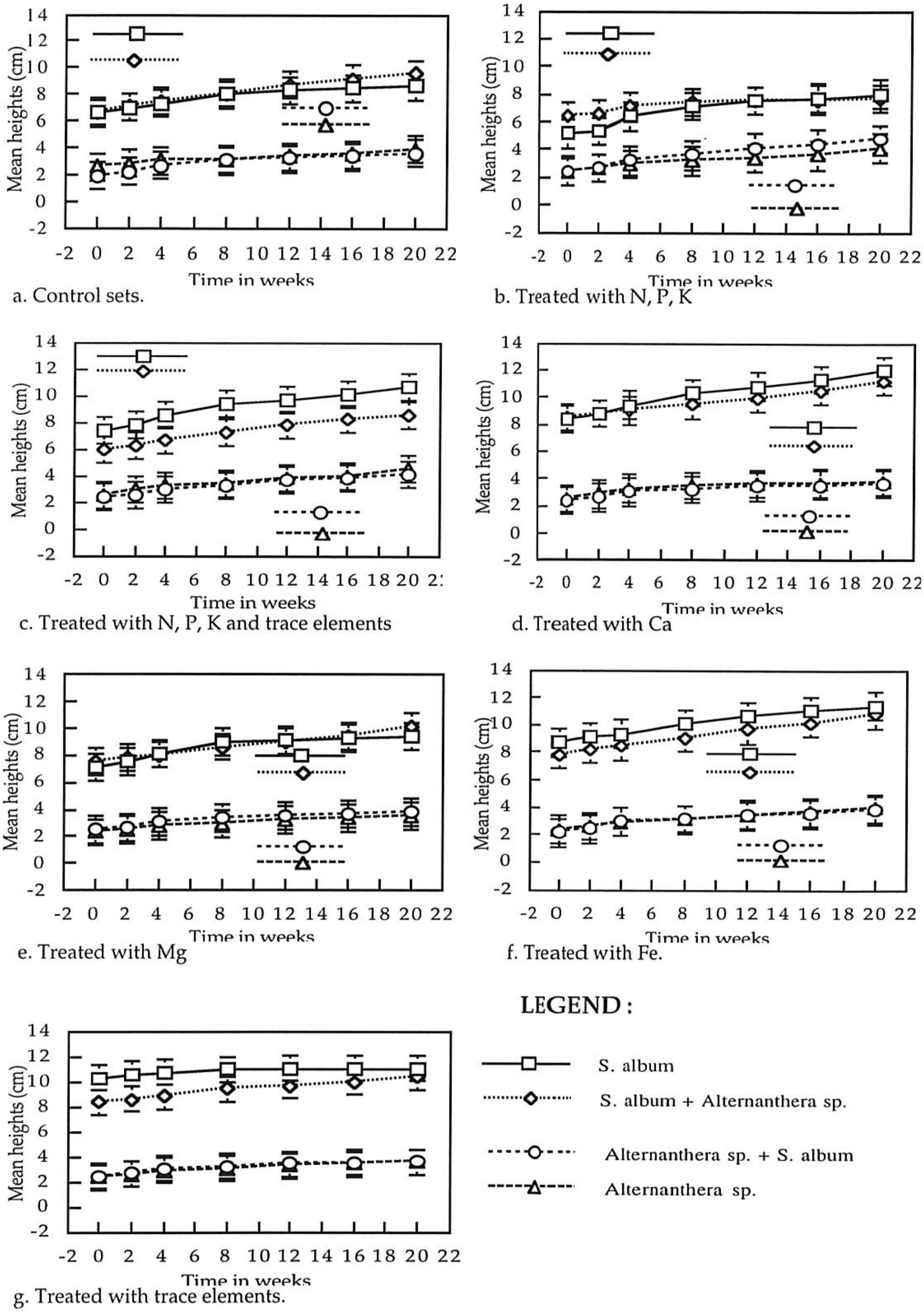
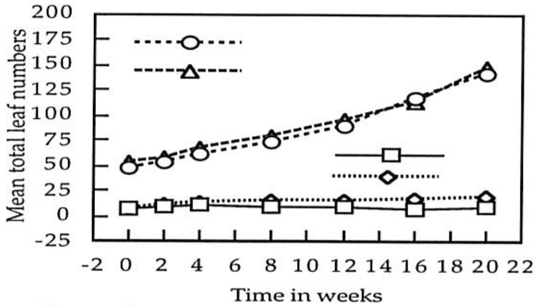
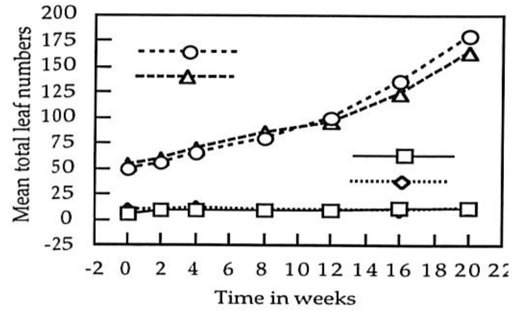


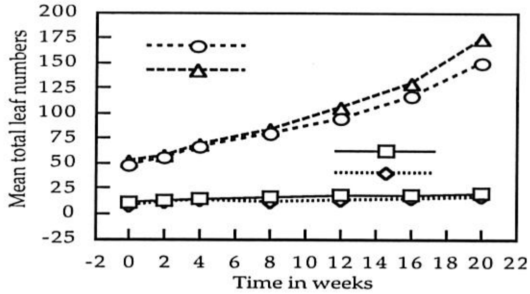
Figure 11. Mean heights of *S. album* (with and without *Alternanthera* sp.), *Alternanthera* sp. (with and without *S. album*) treated with various chemical solutions and control sets (Error bars are standard deviation).

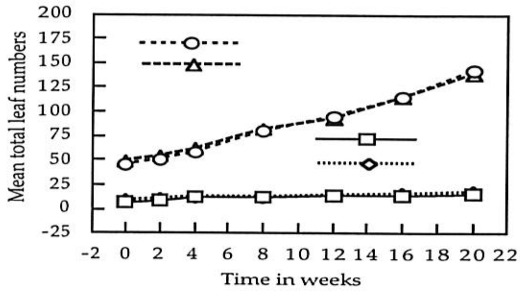


a. Control sets

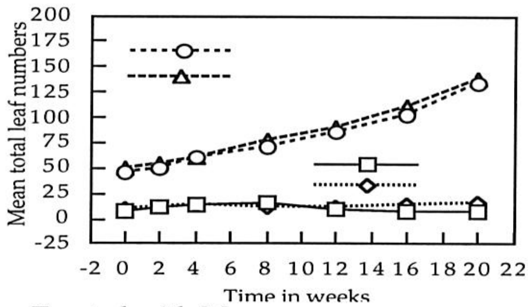


b. Treated with N, P, K

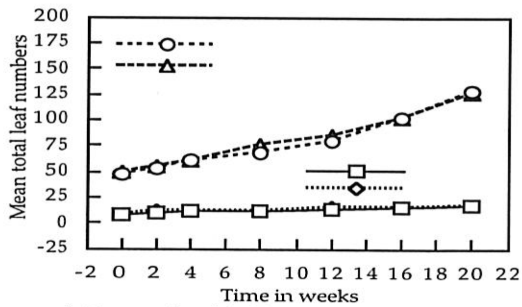




c. Treated with N, P, K and trace elements d. Treated with Ca

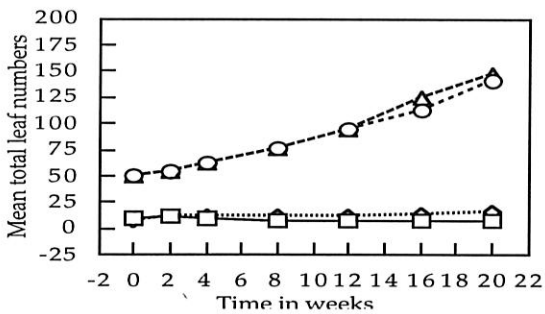


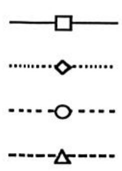
e. Treated with Mg



f. Treated with Fe

LEGEND:





g. Treated with trace elements

Figure 12. Mean total leaf numbers of *S. album* (with and without *Alternanthera* sp.) and *Alternanthera* sp. (with and without *S. album*) treated with various chemical solutions and control sets.

Plant heights

S. album

Starting mean heights differed significantly (Table 25). This was again due to the vagaries of the design (*cf.* Chapter 4). By 12 weeks, differences due to initial height were lost and mean heights were no longer significantly different between treatments. An alternative comparison to attained height is that of height change: mean height at 20 weeks minus mean height at 0 weeks. Unhosted *S. album* seedlings grew most in height when given Ca (Treatment 4). This was followed by N, P, K + trace elements (Treatment 3) and N, P, K (Treatment 2). Presence of *Alternanthera* sp. as a host modified the possible effects of nutrient supply, in that *S. album* plants treated with Fe only (Treatment 13) grew most. Control and the Ca only treatment grew next best.

Design vagaries resulted in differences between treatments in mean height of *S. album* seedlings at the first measurement. *S. album* grown without *Alternanthera* sp., treated with trace elements had tallest mean height from the start until 12 weeks. It was not until 16 weeks that seedlings in the set treated with Ca had caught up (Table 25). *S. album* mean heights in both sets with and without *Alternanthera* sp. and treated with N, P, K were shorter than others over the trial. Chemical nutrients that stimulated *S. album* heights intermediately were: N, P, K and trace element (*S. album* without *Alternanthera* sp.); Fe and trace elements in both sets; and Ca and Mg (*S. album* with *Alternanthera* sp.). All chemical nutrient treatments in both sets appeared to make little incremental height growth over the trial.

By the end of the experiment, there were significant differences in mean heights between treatments in both sets. *S. album* with *Alternanthera* sp. treated with N, P, K was shortest, and differed little from the control, or when treated with N, P, K + trace elements. This also differed little from those grown without *Alternanthera* sp. as control and treated with Mg. Tallest mean heights of *S. album* plants were on those grown without *Alternanthera* sp. treated with Ca. This treatment was not significantly different from sandal grown without *Alternanthera* sp. (treated with Fe; N, P, K + trace elements) and with *Alternanthera* sp. (treated with Ca; Mg; Fe and trace elements).

Table 25. Mean height of *S. album* (n=4) in 14 treatments over the trial (20 weeks), treated with various chemical nutrient elements and control sets.

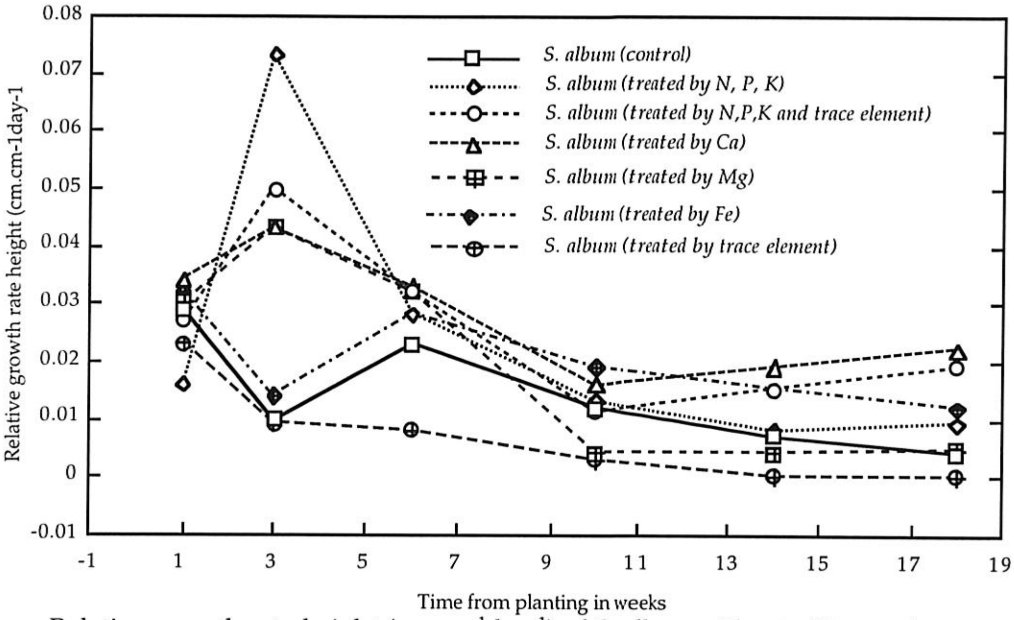
S. album with/without *Alternanthera* sp.	Treated with	0 week	2 weeks	4 weeks	8 weeks	12 weeks	16 weeks	20 weeks
1. no host	Control	6.675 cd	7.075 def	7.350 cdef	8.000 def	8.325 cd	8.525 cde	8.650 cde
2. no host	N,P,K	5.100 e	5.325 g	6.350 f	7.125 f	7.500 d	7.738 e	8.000 e
3. no host	N,P,K, + trace elements	7.425 bcd	7.800 cdef	8.500 bcd	9.400 abcd	9.700 abc	10.125 abc	10.650 abc
4. no host	Ca	8.325 b	8.800 bc	9.400 ab	10.325 a	10.775 ab	11.312 a	11.925 a
5. no host	Mg	7.125 cd	7.550 cdef	8.150 bcde	9.050 bcde	9.175 bcd	9.275 bcde	9.413 bcde
6. no host	Fe	8.700 b	9.150 ab	9.350 ab	10.125 ab	10.650 ab	11.063 ab	11.387 ab
7. no host	Trace elements	10.275 a	10.600 a	10.725 a	10.950 a	11.025 a	11.025 ab	11.025 ab
8. *Alternanthera* sp	Control	6.700 cd	7.100 def	7.525 cdef	8.150 def	8.750 cd	9.212 bcde	9.550 bcde
9. *Alternanthera* sp.	N,P,K	6.375 cde	6.600 efg	7.050 def	7.375 ef	7.513 d	7.575 e	7.713 e
10. *Alternanthera* sp.	N,P,K + trace elements	5.925 de	6.250 fg	6.700 ef	7.150 f	7.813 d	8.212 de	8.500 de
11. *Alternanthera* sp.	Ca	8.475 b	8.750 bc	9.000 b	9.425 abcd	9.887 abc	10.413 abc	11.137 ab
12. *Alternanthera* sp.	Mg	7.600 cd	7.900 bcde	8.050 bcde	8.625 cdef	9.038 bcd	9.462 abcde	10.113 abcd
13. *Alternanthera* sp.	Fe	7.800 bc	8.200 bcd	8.425 bcd	9.000 bcde	9.650 abc	10.137 abc	10.738 ab
14. *Alternanthera* sp.	Trace elements	8.375 b	8.575 bcd	8.825 bc	9.413 abcd	9.663 abc	10.000 abcd	10.363 abcd
F P		2.94 0.004	2.92 0.004	2.29 0.022	2.02 0.043	1.74 0.087	1.66 0.106	1.65 0.110

Column means with same letters are not significantly different, using the Tukey test at the 0.05 level.

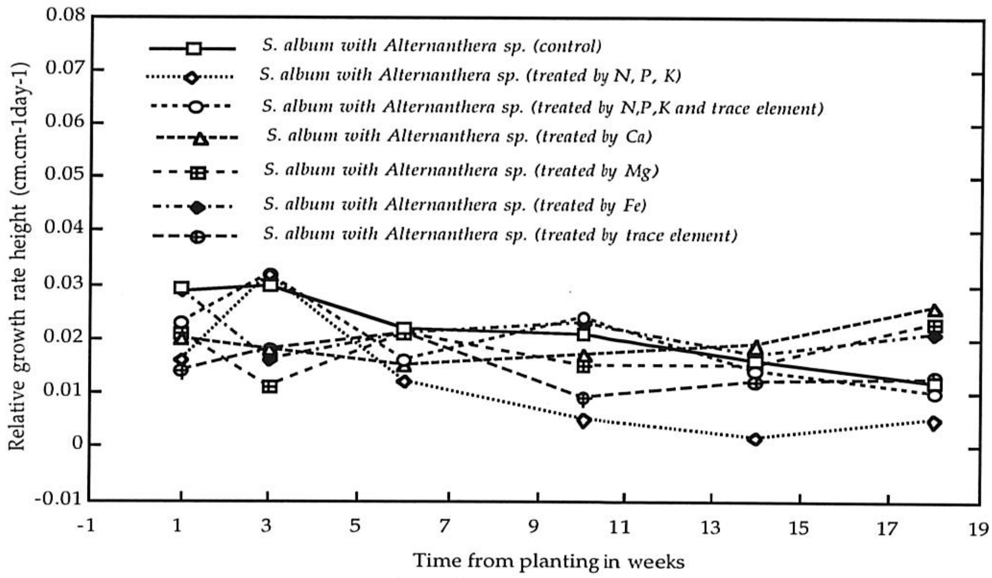
Relative growth rates (RGR) in height of *S. album* were calculated based on Table 25. Mean heights were transformed (log e) to find relative changes in mean heights at 14 and 28 day intervals (Table 26). Relative growth rates in *S. album* heights over the course of the trial are illustrated in Figure 13. This is in two parts, the first shows growth of *S. album* without *Alternanthera* sp. for 7 treatments. The second shows growth of *S. album* with *Alternanthera* sp. in another 7 treatments. Relative growth rate of *S. album* with and without *Alternanthera* sp. in all treatments and the control set differed slightly over the first 6 weeks and after that they increased similarly with time. The RGR of *S. album* alone was much greater in the first 6 weeks than when grown with *Alternanthera* sp.

Table 26. Calculated RGR values of $cm.cm^{-1}day^{-1}$ for changes in mean heights of *S. album* at 14 or 28 day intervals.

Treatment	2-0 wk/14	4-2 wk/14	8-4 wk/28	12-8 wk/28	16-12 wk/28	20-16wk/28
1	0.029	0.010	0.023	0.012	0.007	0.004
2	0.016	0.073	0.028	0.013	0.008	0.009
3	0.027	0.050	0.032	0.011	0.015	0.019
4	0.034	0.043	0.033	0.016	0.019	0.022
5	0.030	0.043	0.032	0.004	0.004	0.005
6	0.032	0.014	0.028	0.019	0.015	0.012
7	0.023	0.009	0.008	0.003	0.000	0.000
8	0.029	0.030	0.022	0.021	0.016	0.012
9	0.016	0.032	0.012	0.005	0.002	0.005
10	0.023	0.032	0.016	0.024	0.014	0.010
11	0.020	0.018	0.015	0.017	0.019	0.026
12	0.021	0.011	0.021	0.015	0.015	0.023
13	0.029	0.016	0.021	0.023	0.017	0.021
14	0.014	0.018	0.021	0.009	0.012	0.013



a. Relative growth rate height ($cm.cm^{-1}day^{-1}$) of *S. album* without *Alternanthera* sp.



b. Relative growth rate ($cm.cm^{-1}day^{-1}$) of *S. album* with *Alternanthera* sp.

Figure 13. Relative growth rate height ($cm.cm^{-1}day^{-1}$) of *S. album* by treatment sets.

Alternanthera sp.

The mean heights of *Alternanthera* sp. increased gradually in all treatments of both sets from an initial 3-4 cm during the course of the experiment (Figure 11). Tallest heights came from *Alternanthera* sp. with *S. album* treated with N, P, K but this was not significantly different from *Alternanthera* sp. alone treated with N, P, K + trace elements (Table 27) at the end of the trial. Shortest heights were in *Alternanthera* sp. alone treated with Mg.

Table 27. Mean height of *Alternanthera* sp. (n=4) in 14 treatments (8 – 21) over the trial (20 weeks), treated with various chemical nutrient elements and control sets.

Alternanthera sp. with/without *S. album*	Treated with	0 weeks	2 weeks	4 weeks	8 weeks	12 weeks	16 weeks	20 weeks
8. with *S. album*	Control	1.975 d	2.25 d	2.75 e	3.15 cde	3.3 cd	3.4375 ef	3.6875 defg
9. with *S. album*	N,P,K	2.45 ab	2.7 abc	3.15 ab	3.575 a	4.1 a	4.3875 a	4.775 a
10. with *S. album*	N,P,K, + trace elements	2.3 bcd	2.55 cd	2.975 abcde	3.225 bcde	3.6 ab	3.75 bc	4.025 bc
11. with *S. album*	Ca	2.375 abc	2.6 abc	3.025 abcde	3.2125 bcde	3.45 bcd	3.5425 cdef	3.65 efg
12. with *S. album*	Mg	2.45 ab	2.625 abc	3.075 abcd	3.3125 abcd	3.5 abc	3.6 cde	3.775 cdef
13. with *S. album*	Fe	2.125 cd	2.4 cd	2.95 bcde	3.1375 cde	3.375 bcd	3.475 def	3.75 cdef
14. with *S. album*	Trace elements	2.425 abc	2.675 abc	3.025 abcde	3.1625 cde	3.3875 bcd	3.475 def	3.6125 efg
15. without *S. album*	Control	2.625 a	2.9 a	3.1 abc	3.225 bcde	3.3875 bcd	3.6 cde	3.9375 bcd
16. without *S. album*	N,P,K	2.35 abc	2.625 abc	2.95 bcde	3.15 cde	3.3375 bcd	3.5875 cde	4.1 b
17. without *S. album*	N,P,K + trace elements	2.55 ab	2.9 a	3.2 ab	3.4 abc	3.7625 a	3.9625 b	4.5625 a
18. without *S. album*	Ca	2.525 ab	2.875 ab	3.275 a	3.4625 ab	3.6 ab	3.6925 cd	3.7875 cdef
19. without *S. album*	Mg	2.275 bcd	2.5 cd	2.775 de	2.975 e	3.1875 d	3.3125 f	3.4625 g
20. without *S. album*	Fe	2.375 abc	2.6 abc	2.9 bcde	3.1 de	3.45 bcd	3.6375 cde	3.9 cde
21. without *S. album*	Trace elements	2.35 abc	2.575 bc	2.85 cde	3.05 de	3.275 cd	3.425 ef	3.5625 fg
F P		1.18 0.326	1.31 0.248	1.03 0.441	1.28 0.261	2.73 0.007	5.47 0.000	7.33 0.000

Column means with same letters are not significantly different using the Tukey test at the 0.05 level.

Plant leaves

S. album

Control unhosted *S. album* with no nutrient addition (Treatment 1) added a mean of only 1.75 leaves over 20 weeks (Table 28). Supply of Mg (Treatment 5) or trace elements (Treatment 7) reduced leaf numbers. Leaf numbers were enhanced most by

Fe (Treatment 6) or Ca (Treatment 4). Presence of *Alternanthera* sp. considerably improved the no-nutrient control (Treatment 8) which added a mean of >11 leaves. Leaf numbers in *S. album* were not reduced by any treatment in the presence of *Alternanthera* sp. Addition of Ca or Fe enhanced leaf numbers most.

At the start, mean leaf numbers on *S. album* seedlings varied from 6 to 12 in sets without *Alternanthera* sp., and from 7 to 10 in sets with *Alternanthera* sp. (Table 28). Mean leaf numbers increased steadily in treatment sets with *Alternanthera* sp. Leaf number declined after 12 weeks in three sets without *Alternanthera* sp.: control, treated with Mg; and trace elements. The greatest mean leaf numbers came from the set where *S. album* was grown alone and treated with N, P, K + trace elements. This was not significantly different from the set where *S. album* was grown with *Alternanthera* sp. as a control (Figure 12).

Table 28. Mean total leaf number of *S. album* (n=4) in 14 treatments over the trial (20 weeks), treated with various chemical nutrient elements and control sets.

S. album with/without *Alternanthera* sp.	Treated with	0 week	2 weeks	4 weeks	8 weeks	12 weeks	16 weeks	20 weeks
1. no host	Control	7.50 bcd	10.00 bc	11.00 bc	10.75 de	9.50 cd	8.25 def	9.25 de
2. no host	N,P,K	6.50 d	9.00 c	10.50 bc	10.25 de	10.25 bcd	11.75 bcdef	12.75 bcde
3. no host	N,P,K, + trace elements	11.75 a	12.50 a	14.25 a	16.50 a	18.25 a	19.00 a	20.75 a
4. no host	Ca	7.00 cd	9.25 bc	12.25 abc	12.50 abcd	13.50 abc	14.50 abc	16.50 abc
5. no host	Mg	8.25 bcd	11.25 abc	13.25 ab	15.50 abc	10.25 bcd	7.50 ef	8.00 e
6. no host	Fe	8.00 bcd	10.50 abc	10.75 bc	12.00 bcd	13.75 abc	15.50 abc	17.75 abc
7. no host	Trace elements	9.00 bcd	11.00 abc	9.50 c	7.00 e	8.00 d	6.75 f	6.75 e
8. *Alternanthera* sp	Control	8.25 bcd	11.50 ab	14.00 a	16.00 ab	15.25 ab	18.25 a	20.00 a
9. *Alternanthera* sp.	N,P,K	9.75 ab	10.50 abc	11.00 bc	9.50 de	9.50 cd	10.75 cdef	12.00 cde
10. *Alternanthera* sp.	N,P,K + trace elements	7.00 cd	10.25 abc	12.00 abc	10.25 de	12.50 bcd	14.50 abc	16.75 abc
11. *Alternanthera* sp.	Ca	8.00 bcd	10.75 abc	12.50 ab	13.25 abcd	14.50 ab	17.00 ab	18.75 ab
12. *Alternanthera* sp.	Mg	9.25 bc	11.00 abc	13.00 ab	12.75 abcd	12.50 bcd	13.75 abcd	15.00 abcd
13. *Alternanthera* sp.	Fe	7.50 bcd	11.25 abc	12.25 abc	12.00 bcd	14.50 ab	15.50 abc	17.75 abc
14. *Alternanthera* sp.	Trace elements	7.50 bcd	11.25 abc	12.50 ab	11.75 cd	11.25 bcd	13.25 abcd	15.00 abcd
F P		1.44 0.182	0.57 0.862	0.87 0.591	1.61 0.122	1.11 0.378	1.68 0.103	1.88 0.062

Column means with same letters are not significantly different using the Tukey test at the 0.05 level.

The relationship between leaf numbers and heights of *S. album* (Table 25 and 28) indicates that increases in leaf number generally followed increases in height. Commonly, it has been reported that there is a spurt in leaf production when *S. album* haustorial connections are successfully made and the parasite is apparently drawing nutrients from the host. To examine whether attained leaf number depends on height, the mean dimensions of all 14 treatments (both sets) and 7 dates of measurements were paired and tested for regression (Figure 14). Significant linear association was found at $p<0.001$. For each 1 cm increase in *S. album* height, leaf numbers increased by a mean of one ($r^2=0.189$).

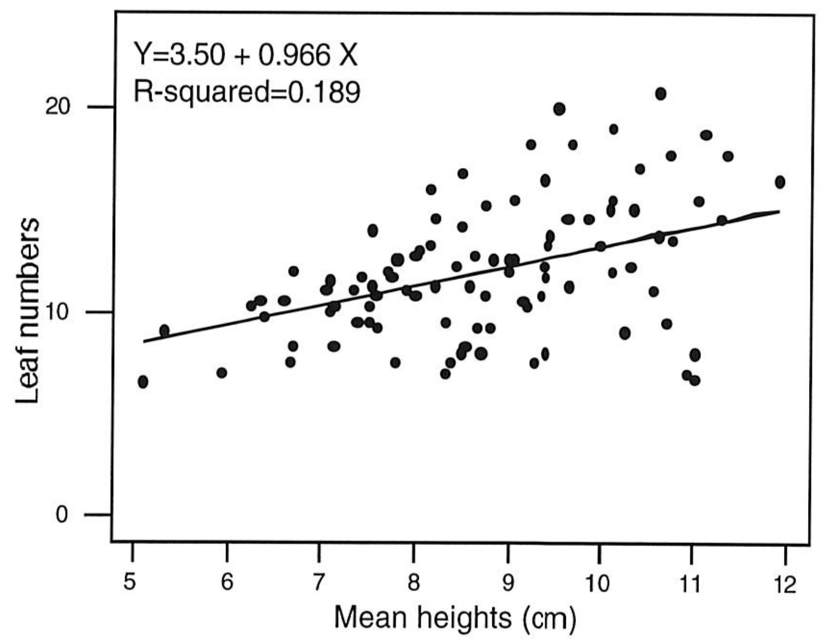


Figure 14. Relationship between mean heights and mean leaf numbers of *S. album* in all treatment sets over the trial.

Although differences in mean total leaf number at 20 weeks almost reached significance (p=0.062, Table 28), analysis of variance at harvest revealed that *S. album* mean leaf areas among the 14 treatments differed less (p=0.113), not attaining significance (Table 29). The smallest leaf area was found with S. *album* grown alone as the control set. The biggest leaf area at the end of the trial was *S. album* grown with *Alternanthera* sp. treated with Fe.

Harvest leaf areas in unhosted *S. album* (Table 29) with Mg or trace elements showed no improvement over the control. In contrast, with Fe (Treatment 6) or Ca (Treatment 4), leaf areas were 6.7 x and 5.5 x greater than the control respectively. Presence of *Alternanthera* sp. improved *S. album* control leaf area by 3.9 x (Treatment 8 versus Treatment 1); with trace elements by 5.5 x (Treatment 14 versus Treatment 7) and with Mg by 3.9 x (Treatment 12 versus Treatment 5). Greatest leaf area was again with Fe (Treatment 13). The host effect was poorest with N, P, K (Treatment 9) and Ca (Treatment 11) where leaf area was lower than with unhosted *S. album* given those nutrients.

Table 29. Mean leaf area dimension (cm^2) of *S. album* (n=4) in 14 treatments after harvest.

S. album with/without *Alternanthera* sp.	Treated with	Leaf area
1. without *Alternanthera* sp.	Control	3.54 e
2. without *Alternanthera* sp.	N,P,K	6.81 de
3. without *Alternanthera* sp.	N,P,K, + trace elements	8.18 cde
4. without *Alternanthera* sp.	Ca	19.35 abc
5. without *Alternanthera* sp.	Mg	3.43 e
6. without *Alternanthera* sp.	Fe	23.84 ab
7. without *Alternanthera* sp.	Trace elements	3.66 e
8. with *Alternanthera* sp	Control	13.67 bcde
9. with *Alternanthera* sp.	N,P,K	3.80 e
10. with *Alternanthera* sp.	N,P,K + trace elements	12.69 bcde
11. with *Alternanthera* sp.	Ca	17.18 abcd
12. with *Alternanthera* sp.	Mg	13.50 bcde
13. with *Alternanthera* sp.	Fe	27.01 a
14. with *Alternanthera* sp.	Trace elements	20.07 abc
F		**1.64**
P		**0.113**

Column means with same letters are not significantly different using the Tukey test at the 0.05 level.

Observations at the end of the experiment showed that *S. album* leaf colour (Royal Horticultural Society Charts) ranged from yellow green 144A (dark), 144B (middle), 144C (light), to 146C (dark green) in both sets in all treatments. Old marginal leaf colour was red purple 59A possibly due to N or P deficiency. No patterns of colour differences could be associated with application of different nutrient solutions.

Alternanthera sp.

Foliage development on *Alternanthera* sp. was broadly similar across all foliar nutrient treatments with and without *S. album* (Table 30). After 20 weeks, *Alternanthera* sp. foliage had increased most with N, P, K treatments, in respect to the presence of *S. album*. Fe and Ca may have depressed *Alternanthera* sp. foliage growth as those had fewest leaves.

Analysis of variance revealed large significant differences in *Alternanthera* sp. leaf areas (Table 31). The biggest leaf areas were on *Alternanthera* sp. grown without and with *S. album* treated with N, P, K. *Alternanthera* sp. leaf areas with each of Ca, Mg, Fe or trace elements were less than those of the controls with reduced leaf numbers.

Table 30. Mean total leaf number of *Alternanthera* sp. (n=4) in 14 treatments (8–21) over the trial, treated with various chemical nutrient elements and control sets.

Alternanthera sp. with/without *S. album*	Treated with	0 weeks	2 weeks	4 weeks	8 weeks	12 weeks	16 weeks	20 weeks
8. with *S. album*	Control	48.0 cde	53.75 cd	61.25 de	74.25 ef	88.75 bcd	117.25 bcd	141.5 cd
9. with *S. album*	N,P,K	48.75 cd	56.0 abc	65.75 bc	79.5 bcd	99.0 ab	136.0 a	178.25 a
10. with *S. album*	N,P,K, + trace elements	48.75 cd	54.5 bcd	65.75 bc	78.75 bcde	93.25 bc	116.5 bcde	149.5 bc
11. with *S. album*	Ca	46.0 de	51.5 de	59.0 e	79.5 bcd	95.0 abc	115.75 bcde	142.0 cd
12. with *S. album*	Mg	45.25 e	50.0 e	59.75 de	71.25 fg	85.25 cd	102.0 de	134.0 cd
13. with *S. album*	Fe	48.0 cde	52.75 de	61.25 de	68.25 g	79.75 d	101.5 e	127.5 d
14. with *S. album*	Trace elements	49.25 bc	55.0 bc	63.0 cd	75.75 def	95.0 abc	113.0 cde	141.25 cd
15. without *S.album*	Control	53.0 ab	57.75 ab	66.75 ab	79.75 bcd	96.25 abc	112.75 cde	148.0 bc
16. without *S.album*	N,P,K	53.75 ab	59.25 a	69.5 a	84.75 a	95.25 abc	123.5 abc	163.25 abc
17. without *S. album*	N,P,K + trace elements	52.0 ab	57.0 abc	68.0 ab	83.5 ab	104.5 a	129.0 abc	172.5 a
18. without *S. album*	Ca	49.25 bc	54.0 cd	62.5 cde	81.5 abc	93.5 abc	115.0 bcde	138.25 cd
19. without *S. album*	Mg	49.0 c	53.75 cd	59.25 e	76.0 def	90.5 bcd	110.0 cde	137.25 cd
20. without *S. album*	Fe	49.5 bc	54.25 cd	60.75 de	74.5 ef	85.5 cd	102.25 de	126.25 d
21. without *S. album*	Trace elements	50.25 bc	54.5 bcd	61.5 de	76.75 cde	93.5 abc	124.5 abc	146.5 bc
F P		2.79 0.006	2.10 0.035	3.30 0.002	3.46 0.001	1.27 0.268	0.75 0.085	2.95 0.004

Column means with same letters are not significantly different using the Tukey test at the 0.05 level.

Table 31. Mean leaf area dimension (cm^2) of *Alternanthera* sp. (n=4) in 14 treatments (8 – 21) after harvest.

Alternanthera sp. with or without *S. album*	Treated with	Leaf area
8. with *S. album*	Control	113.54 c
9. with *S. album*	N,P,K	204.44 b
10. with *S. album*	N,P,K, + trace elements	115.1 c
11. with *S. album*	Ca	35.05 e
12. with *S. album*	Mg	56.5 e
13. with *S. album*	Fe	45.92 e
14. with *S. album*	Trace elements	41.1 e
15. without *S. album*	Control	82.93 d
16. without *S. album*	N,P,K	230.62 a
17. without *S. album*	N,P,K + trace elements	134.73 c
18. without *S. album*	Ca	48.91 e
19. without *S. album*	Mg	38.18 e
20. without *S. album*	Fe	47.79 e
21. without *S. album*	Trace elements	47.65 e
F P		**28.88** **0.000**

Column means with same letters are not significantly different using the Tukey test at the 0.05 level.

Observation indicated *Alternanthera* sp. leaf colours mostly ranged from red purple 57C-57D when grown with *S. album* to red purple 66C in control, grown alone. *Alternanthera* sp. grown without *S. album* had leaf colours red purple 57C-57D (treated with N, P, K; N, P, K and trace element; Ca) and red purple 66C-66D (control, treated by Mg, Fe and trace element).

Plant roots

S. album

Observation of root numbers, haustoria and root area on harvested plants showed significant differences in root numbers (p=0.08) and haustoria (p=0.003) between nutrient treatments, but not amongst mean root areas (p=0.16) on *S. album* (Table 32). Greatest root numbers, largest root area and most haustoria were found on *S. album* hosted to *Alternanthera* sp. and treated with Fe. Second greatest values were with Ca. This pattern was similar in unhosted *S. album*, with some differences in ranking.

At the other extreme, N, P, K treatment depressed root number and root area relative to the control on both hosted and unhosted *S. album*. N, P, K was also associated with low haustoria number on hosted *S. album*. Both Mg and trace elements reduced root number and root area on unhosted *S. album* but these reductions were not apparent on plants hosted to *Alternanthera* sp.

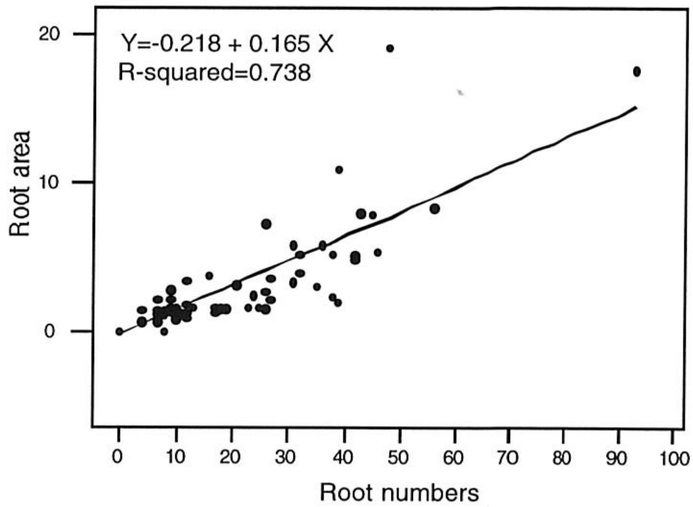
Table 32. Total root numbers, root areas (cm^2) and haustoria numbers in 14 treatments of *S. album* (n=4) after 20 weeks in the nursery.

S. album with/without *Alternanthera* sp.	Treated with	Root number	Root area	Haustoria
1. without *Alternanthera* sp.	Control	15.75 cde	1.775 cd	2.500 ef
2. without *Alternanthera* sp.	N,P,K	13.75 cde	1.187 cd	3.250 def
3. without *Alternanthera* sp.	N,P,K, + trace elements	27.50 bcd	2.638 cd	7.500 bcd
4. without *Alternanthera* sp.	Ca	27.75 bcd	4.512 abc	6.500 cde
5. without *Alternanthera* sp.	Mg	12.75 de	0.978 d	2.500 ef
6. without *Alternanthera* sp.	Fe	24.50 bcde	4.227 abcd	5.750 def
7. without *Alternanthera* sp.	Trace elements	13.00 de	1.660 cd	1.750 f
8. with *Alternanthera* sp	Control	25.50 bcde	2.430 cd	5.250 def
9. with *Alternanthera* sp.	N,P,K	11.50 e	1.530 cd	2.750 ef
10. with *Alternanthera* sp.	N,P,K + trace elements	12.50 de	3.213 bcd	3.500 def
11. with *Alternanthera* sp.	Ca	34.50 ab	6.633 ab	11.500 ab
12. with *Alternanthera* sp.	Mg	33.00 ab	3.577 bcd	8.750 bcd
13. with *Alternanthera* sp.	Fe	44.50 a	7.293 a	14.500 a
14. with *Alternanthera* sp.	Trace elements	28.75 bc	6.640 ab	11.000 abc
F		1.80	1.49	3.10
P		0.076	0.160	0.003

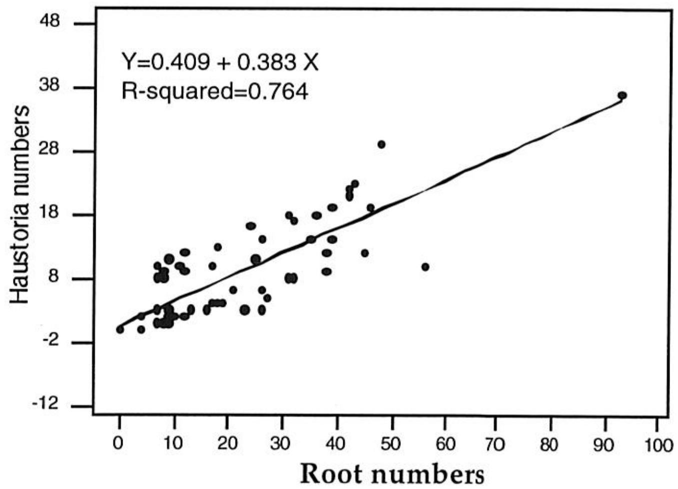
Column means with same letters are not significantly different using the Tukey test at the 0.05 level.

There is a general correspondence between the root parameters examined at the time of harvest (Table 32). Clearly, there is likely to be a greater root area with more roots present. Similarly, the chance of haustoria developing is likely to be increased with presence of more roots. Measurements from harvested plants were paired and tested for linear regression. Mean root area was found to increase by 0.17 cm^2 for each additional root over the range illustrated (Figure 15 a). With the calculated value of r=0.859, this is highly significant (n=56, df=54, at p=0.001, r=0.429). Similarly, mean haustoria number increases by 1 for each additional 2.61 roots (Figure 15 b), and r=0.874.

Correlation analysis (Appendix 17) using treatment means, suggests root area is highly correlated with leaf area (r=0.930, p=0.01) and mean dry weight (r=0.899, p=0.01) in unhosted sets and with leaf area (r=0.894, p=0.01) but not dry weight in hosted sets. For all treatment means, the strongest correlation of root area is with leaf area (r=0.890, p=0.001). Haustoria depend strongly on number of roots and are associated less strongly with root area in the unhosted condition. Presence of the host leads to strong correlation of haustoria with each of root number, root area and also leaf area.



a.Relationship between root area and total roots of *S. album*.



b. Relationship between haustoria and root numbers of *S. album*.

Figure 15. Relationships between: a. root areas; and b. haustoria; and root numbers in *S. album*.

***Alternanthera* sp.**

There were significant differences in root numbers and root area of *Alternanthera* sp. after 20 weeks in the nursery. Root areas were not significantly different between the treatments in the sets grown with *S. album* (Table 33). The greatest root number was on *Alternanthera* sp. grown with *S. album* treated by N, P, K and trace elements. *Alternanthera* sp. root areas grown without *S. album* in 4 treatments (control, N, P, K; N, P, K and trace element; and Ca) were larger than *Alternanthera* sp. grown with *S. album*. The smallest root numbers came from *Alternanthera* sp. as control.

Table 33. Total root numbers, root areas (cm^2) and haustoria numbers in 14 treatments (8 – 21) of *Alternanthera* sp. (n=4) after 20 weeks in the nursery.

Alternanthera sp. with or without *S. album*	Treated with	Root number	Root area
8. with *S. album*	Control	120.5 def	30.443 b
9. with *S. album*	N,P,K	142.0 b	31.158 b
10. with *S. album*	N,P,K, + trace elements	156.75 a	25.597 b
11. with *S. album*	Ca	115.0 ef	28.298 b
12. with *S. album*	Mg	132.0 bcd	25.685 b
13. with *S. album*	Fe	127.0 cde	22.75 b
14. with *S. album*	Trace elements	140.25 bc	27.445 b
15. without *S. album*	Control	85.25 h	48.458 a
16. without *S. album*	N,P,K	93.75 gh	46.715 a
17. without *S. album*	N,P,K + trace elements	124.75 de	42.732 a
18. without *S. album*	Ca	140.25 bc	51.423 a
19. without *S. album*	Mg	107.0 fg	28.103 b
20. without *S. album*	Fe	124.25 de	27.27 b
21. without *S. album*	Trace elements	131.5 bcd	28.183 b
F P		7.83 0.000	4.85 0.000

Column means with same letters are not significantly different using the Tukey test at the 0.05 level.

Harvest weights

S. album

The pattern of mean harvest weights between treatments is of considerable interest, but the differences between means did not reach significance, despite a more than three-fold increase among unhosted and hosted sets (Table 34). Unhosted control *S. album* produced greater biomass than each of treatments with N, P, K; N, P, K + trace elements; Mg or trace elements. This depression was greaterst with Mg. Addition of both Fe and Ca stimulated growth of unhosted seedlings, by 1.5 x and 1.3 x over that of the control, respectively.

Presence of *Alternanthera* sp. in the pot did not improve unfertilised seedling weight (control). In all nutrient treatments a benefit appeared with presence of the host.

Improvement in weight associated with host presence was generally only between 5 and 14 % in weight. The exception was that growth of plants given Mg was enhanced by 2.4 x with *Alternanthera* sp. present. Despite this general enhancement with host presence, all except Fe and Ca treatments remained less than the hosted control with no nutrient additions.

Correlation analysis sought the most important contribution to dry weight among measured attributes (Appendix 17). This was found to be root area in the unhosted treatments (r=0.899, p=0.01); root number in hosted treatments (r=0.876, p=0.01) and leaf area for all 14 treatments (r=0.828, p=0.001).

Table 34. Mean dry weights in 14 treatments of *S. album* (n=4) after 20 weeks in the nursery.

S. album with/without *Alternanthera* sp.	Treated with	Wet weight	Dry weight	Moisture
1. without *Alternanthera* sp.	Control	0.3475 d	0.3257 abc	0.0218 (6.273%)
2. without *Alternanthera* sp.	N,P,K	0.6000 cd	0.1535 c	0.4465 (74.42%)
3. without *Alternanthera* sp.	N,P,K, + traces	0.9000 bcd	0.2348 bc	0.6652 (73.91%)
4. without *Alternanthera* sp.	Ca	1.5250 ab	0.4108 ab	1.1142 (73.06%)
5. without *Alternanthera* sp.	Mg	0.3825 d	0.1322 c	0.2503 (65.44%)
6. without *Alternanthera* sp.	Fe	1.9250 a	0.4902 a	1.4348 (74.53 %)
7. without *Alternanthera* sp.	Trace elements	0.5250 cd	0.2167 bc	0.3083 (58.72%)
8. with *Alternanthera* sp	Control	0.9000 bcd	0.3173 abc	0.5827 (64.74%)
9. with *Alternanthera* sp.	N,P,K	0.4250 d	0.1720 c	0.2530 (59.53%)
10. with *Alternanthera* sp.	N,P,K + traces	0.9250 bcd	0.2555 bc	0.6695 (72.38%)
11. with *Alternanthera* sp.	Ca	1.3750 abc	0.4325 ab	0.9425 (68.55%)
12. with *Alternanthera* sp.	Mg	1.1000 abcd	0.3148 abc	0.7852 (71.38%)
13. with *Alternanthera* sp.	Fe	1.9000 a	0.5288 a	1.3712 (72.17%)
14. with *Alternanthera* sp.	Trace elements	1.6750 ab	0.2475 bc	1.4275 (85.22%)
F P		1.52 0.149	1.26 0.275	

Column means with same letters are not significantly different using the Tukey test at the 0.05 level.

Alternanthera sp.

Comparison of mean dry weights of the 14 treatments in both sets indicated that there were significant differences. Mean dry weight of *Alternanthera* sp. without *S. album* treated by Ca was the heaviest. *Alternanthera* sp. with *S. album* treated with Ca was the lightest in mean dry weight.

Table 35. Mean dry weight in 14 treatments (8 – 21) of *Alternanthera* sp. (n=4) after 20 weeks in the nursery.

Alternanthera sp. with or without *S. album*	Treated with	Wet weight	Dry weight	Moisture
8. with *S. album*	Control	17.975 (c)	2.975 (bcde)	15.0 (83.449%)
9. with *S. album*	N,P,K	31.425 (a)	3.375 (bc)	28.05 (89.26%)
10. with *S. album*	N,P,K, + trace element	20.2 (c)	2.9 (bcdef)	17.3 (85.644%)
11. with *S. album*	Ca	10.2 (d)	1.8 (i)	8.39 (82.255%)
12. with *S. album*	Mg	12.45 (d)	2.175 (fghi)	10.275 (82.53%)
13. with *S. album*	Fe	9.5 (d)	1.9 (hi)	7.6 (80%)
14. with *S. album*	Trace element	11.5 (d)	2.05 (ghi)	9.45 (82.174%)
15. without *S. album*	Control	12.425 (d)	2.6 (defgh)	9.825 (79.074%)
16. without *S. album*	N,P,K	25.55 (b)	3.3 (bcde)	22.25 (87.084%)
17. without *S. album*	N,P,K + trace element	18.425 (c)	3.55 (b)	14.875 (80.73%)
18. without *S. album*	Ca	21.55 (c)	4.475 (a)	17.075 (79.23%)
19. without *S. album*	Mg	11.325 (d)	2.35 (efghi)	8.975 (79.25%)
20. without *S. album*	Fe	11.4 (d)	2.55 (efghi)	8.85 (77.63%)
21. without *S. album*	Trace element	13.15 (d)	2.7 (cdefg)	10.45 (79.47%)
F P		11.54 0.000	3.98 0.000	

Column mean with same letters not significantly different using the Tukey test at the 0.05 level.

Discussion

Inadequate segregation of *S. album* sizes assigned to treatments and a lack of replicates may have been responsible for little significance amongst the parameters. Nevertheless, patterns of difference suggest trends. These may be further explored in a larger, repeat trial.

This experiment has shown that *S. album* grows better with *Alternanthera* sp. than when alone, in the absence of nutrients to 20 weeks. Most leaves came from unhosted *S. album* treated with N, P, K + trace elements. This suggests that *S. album* is able to uptake minerals *via* its leaf system. High K concentrations and K/Ca ratios occur in pre-parasitic seedlings of *S. album*. Whilst at later stages it may obtain N, P and K from hosts, for at least 3 months nutrients can be adequately obtained from the rooting medium (Barrett and Fox 1997), especially when *S. album* is grown without *Alternanthera* sp. Poor health condition of *S. album* when grown alone, and lacking individual nutrients indicates the importance of seed as a nutrition source to support growth of seedlings. Sandalwood kernels provide nutrition, which can support growth of small seedlings for 3 months (Barrett and Fox 1997). Kernels contain sources of P, Mg, Cu, Zn, N, K, Ca and Fe (Srinivasan *et al.* 1992, Shankara Narayana and Parthasarathi 1985). Even though *S. album* is capable of photosynthesis and some nutrient uptake from soil, it requires nutrients from hosts for survival, and at least some essential nutrients (N, P, K, Na, Ca, Cu, water and basic amino acids) are known to be transferred from the host roots.

Growth in height and leaf numbers in control sets and all nutrient treatments was at about the same rate at least up to 16 weeks. The hemiparasitic habit of *S. album* is notorious for uneven growth and poor early survival, as the species depends on early host connections. Even though sandalwood seedlings are reported as able to survive up to 3 years (Rama Rao 1911, Wijesuriya and Fox 1985, Widiarti 1989), seedling plants observed are often in poor health (Nagaveni and Srimathi 1985). During the pre-parasitic period cotyledon nutrients are available (Loneragan 1990) with some from the growing medium or soil. From the cotyledons, seeds derive four main groups of phosphate containing compounds: these are nucleic acids, inorganic P compounds, phosphatides and phytates (Lolas and Markakis 1975). Phytates act as phosphate sources, inositol and cations (monovalent and divalent). These are mobilised to support growth of the developing seedling until the root system is formed (Lott 1984). Earlier research has indicated that moisture and some nutrients: N, P, K, Mg, Ca, Fe, Cu, Zn and basic amino acids are transferred from the host (Rangaswamy *et al.* 1986; Sreenivasa Rao 1933; Ramaiah *et al.* 1962; Struthers *et al.* 1986) enabling maintenance of growth after exhaustion of cotyledons. Early haustorial attachment is essential to longer-term survival.

Addition of Mg; N, P, K or trace elements depresses growth in root characteristics of unhosted *S. album* but this effect is ameliorated in presence of *Alternanthera* sp. as a host. *S. album* grown alone exhibited increased leaf fall after 4 weeks (control), after 8 weeks (treated with Mg) and after 2 weeks (trace elements). This might be related to deficiencies of iron. *S. paniculatum*, *S. album* and *S. haleakalae* began to produce small and chlorotic leaves with each new flush of growth (Hirano 1977) in response to iron deficiencies. When seedlings were provided with chelated iron, leaves became green, the tips of seedlings started new shoot growth, and without iron seedlings died. Barrett and Fox (1997) indicate lack of nutrients (N, K and P) curtails growth at about 3 months. On the other hand, Struthers *et al.* (1986) found that growing *S. spicatum* in hydroponic culture without Ca, resulted in seedlings dying within 3 weeks.

There were significant differences in leaf numbers at the end of the trial. However, two treatments (*S. album* alone treated with N, P, K + trace elements and control set where *S. album* was grown with *Alternanthera* sp.) were greater than others. This indicates that some essential nutrients are able to be taken up from the leaf for *S. album* treated with N, P, K + trace elements; while with *S. album* grown with *Alternanthera* sp., some essential nutrients are likely transferred from *Alternanthera* sp.

The most important observation is that Fe and Ca as added nutrients do produce gains in growth when added to unhosted seedlings of *S. album*. Presence of *Alternanthera* sp. as a host reduces these effects. The combination of N, P, K is largely ineffective. Although it may stimulate the host, differences in unhosted seedlings appeared negative.

Beneficial effects of Fe nutrient solution were shown in this experiment in terms of increased leaf area, total root number, root area, haustoria development and dry weight of *S. album* when grown with *Alternanthera* sp. Also the colour of leaves was yellow green. The newer and younger leaves were not affected by chlorotic symptoms either interveinally or marginally. Deficiency of iron only affects upper leaves, showing interveinal chlorosis with green veins in a fairly regular feather pattern (Barrett *et al.* 1993). Some reddening of leaf margins and petioles appear, whereas leaf area is normal. Root structure appears normal with spreading, fine roots and haustoria developed. Treatment with Fe nutrient solution stimulated root growth and haustoria development.

Beneficial effects of nutrient solutions were shown on *Alternanthera* sp. root growth: root numbers (N, P, K + trace elements); root area (N, P, K; N, P, K + trace elements and Ca). Significantly different heights, leaf numbers and leaf areas of *Alternanthera* sp. came from *Alternanthera* sp. grown alone treated with N, P, K. The heaviest dry weight was *Alternanthera* sp. alone treated with Ca and the lightest was *Alternanthera* sp. grown with *S. album* treated with Ca. This suggests that *S. album* draws other nutrients from *Alternanthera* sp. to support its growth and survival. There is a balance in growth between parasite and host (Watkinson and Gibson 1988), lightest dry weight of *Alternanthera* sp. grown with *S. album* indicates that *S. album* damages *Alternanthera* sp. This also means that *S. album* parasitizes *Alternanthera* sp. for other nutrients to sustain growth (Radomiljac 1998).

Dry weights of *S. album* when grown with and without *Alternanthera* sp. treated with Fe were significantly greater than other treatments. Heaviest *S. album* dry weight when grown with *Alternanthera* sp. treated with Fe indicates that other supplementary nutrients did not significantly influence the growth of *S. album*. This indicates *Alternanthera* sp. may have ameliorated the effect of *S. album* growth. In other words, some nutrients are transferred from *Alternanthera* sp. to *S. album* (Radomiljac 1998). It can be concluded that supplementary nutrients did not significantly influence the growth and the survival of *S. album*. In contrast, *S. album* captured nutrients from *Alternanthera* sp.

Lack of Ca in nutrient solution caused *S. album* seedlings to die prematurely or at least survive in poor health conditions, while without supplementary N, Fe and micronutrients, growth was significantly reduced (Wijesuriya 1984, Struthers *et al.* 1986). Poor health of *S. album* when grown alone and good health when associated with *Alternanthera* sp. lacking individual nutrients indicates that *S. album* may obtain N, P and K from *Alternanthera* sp. (Barrett and Fox 1997).

Conclusion

S. album is able to take up supplementary nutrient solutes via its leaf system and can survive in a sterile medium, without a host, for at least 3 months. During this period *S. album* seedlings grow poorly, and are dependent on cotyledon resources to support growth. A range of different supplementary nutrient solutes did not significantly stimulate growth of *S. album* seedlings.

Omission of some supplementary nutrients and the lack of individual nutrient, result in increased leaf fall. *S. album* seedlings grown alone in a sterile medium without supplementary nutrient showed increased leaf fall at about 4 weeks after planting. Mg nutrient solution also effected leaf fall at about 8 weeks and trace elements at about 2 weeks. Ca nutrient solution promoted height of *S. album* when grown alone better than other nutrient solutions. Relative growth rate of *S. album* grown without *Alternanthera* sp. was faster in the first 6 weeks than when associated with *Alternanthera* sp. Nutrient supplements did not significantly affect *S. album* leaf area. *S. album* grown with *Alternanthera* sp. performed best when treated with Fe in terms of greatest root numbers, largest root area, most haustoria development and heaviest dry weight.

It is concluded that *S. album* can effectively depend on *Alternanthera* sp. as a pot-host for some essential nutrients to maintain growth after exhaustion of the cotyledons. Supplementary nutrient solutes did not stimulate the growth and the survival of *S. album*. Essential nutrients are transferred from *Alternanthera* sp.

6. Observations on Potential hosts of *S. album*

Introduction

The most popular species of sandalwood, *S. album* (Indian sandalwood), is characterised by early onset of heartwood development, high santalol oil content, a faster growth rate and larger tree form than other sandalwood species (Shea *et al.* 1998). The highest quality of oil is produced from heartwood of both stem and root. This oil is one of the most valuable in the world.

S. album grows as a forest tree in regions that vary from seasonally dry monsoon climates (India, eastern Indonesia, and Vanuatu) to sub-tropical climates with almost uniform rainfall (Hawaii and New Caledonia). Climate refers to the meteorological conditions in a given localised area over a period of seasons and years. Temperature varies with latitude and altitude, generally becoming higher when closer to the equator or closer to sea level. Thermal fluctuations occur daily and seasonally. Plants often display different levels of tolerance at different stages in their life cycle, generally becoming more tolerant as they mature (Knight 1965). Temperature influences the metabolic rate of the plants (McCloud and Bula 1973). The rate of maturation and growth is directly related to temperature, causing plants to bloom at shorter heights in hotter regions. Humidity is directly related to temperature; the higher the temperature, the more water may exist as atmospheric moisture.

Other conditions related to the climate include rainfall and sunlight. Rainfall is the main and most important source of precipitation in tropical and temperate regions (Knight 1965, Fitzpatrick and Nix 1970). The type of rainfall depends on wind, temperature and air pressure (Knight 1965). Rainfall can, in turn, affect plant growth. Light drizzle is generally not absorbed into the soil due to evaporation. Light steady rain is very effective, soaking and replenishing the soil. Only about 75% of the visible light available to the plant is absorbed. Much of this is converted into long wavelength radiation and radiated or used in evaporation (Spedding 1971). Excess light does not increase photosynthesis (Jewiss 1967). Light is only a fragment of the solar radiation and the only beneficial part. Too much exposure to lower frequency radiation will kill plants while higher frequency radiation can cause mutation and dwarfing in plants. The photoperiod may affect both reproductive and vegetative growth. Plants may be short-day or long-day flowering.

Sandalwood is primarily a tree of dry deciduous forests where it is prone to fire damage. Fire is one of sandalwood's worst enemies; sandalwood reshoots after being affected by fire, and it is therefore necessary either to cut back the young plant or cut the older tree and leave it for about a year to develop shoots, the best of which may then be chosen (Azais 1995). In general, it is absent from hill slopes and grassy banks that are prone to annual fire; however, when these areas are protected from fire, sandalwood appears again. Similarly, under moist deciduous conditions when a site becomes more mesic, sandalwood recedes to drier portions. Sandalwood has a number of main associates in the top canopy (Rai 1990). These include: *Terminalia tomentosa, T. chebula, Anogiessus latifolia, Sapindus trifoliatus, Diospyros melanoxylon, Albizia lebbeck, A. odoratissima, A. amara, Chloroxylon swietenia, Feronia elephantum, Limonia acidissima, Zizyphus xylopyrus, Grewia tilaefolia, Bridelia retusa, Ixora parviflora, Pterocarpus marsupium, Dendrocalamus strictus, Bauhinia racemosa, Acacia sundra.* Undergrowth includes *Carissa carandus, Dodonea viscosa, Randia dumetorum, Cassia fistula, C. auriculata, Lantana camara, Zizyphus oenoplea, Flacourtia montana.*

In India, the main associates of forests with *S. album* in Madhya Pradesh are categorised into 3 groups (Tiwari and Pandey 1998). Firstly, in the upper canopy: *Tectona grandis, Lannea coromandelica, Boswellia serrata, Madhuca latifolia, Albizia lebbeck, Terminalia tomentosa, Diospyros melanoxylon, Anogeissus latifolia, Lagerstroemia parviflora* and *Adina cordifolia*. Secondly, in the lower canopy: *Cassia fistula, Aegele marmelose, Buchanania lanzam, Dendrocalamus strictus,* and *Sarcopetalum tomentosum*. Finally, in the understorey: *Cassia spinarum, Gymnosporia montana, Zyzyphus xylopyra, Randia dumentotrum, Lantana camara, Cassia tora, Ageratum conyzoides* and several grass species and small herbs.

As a hemi-parasitic species *S. album* is able to develop haustoria on its roots and is usually partially parasitic on the roots of other plants. It needs a range of hosts in the natural condition to support its survival (Sinha 1961). Some researchers suggest that some sandalwoods, including *S. album,* are not always obligate parasites. For example, some haustoria-less *S. album* are reported in the nursery stage (Nagaveni and Srimathi 1985). However, it is generally accepted that *S. album* needs hosts to provide mineral nutrition and also shade when young (Barrett and Fox 1994, Fox and Barrettt 1995). The nature of mineral solutes provided by hosts varies (Pate *et al.* 1991). It is believed that N, K, Na, P and water (Sen-Sarma 1977; Struthers *et al.* 1986), and amino acids (Srimarthi *et al.* 1961) are supplied by hosts.

In India, the haustorium can grow to a fairly large size. The haustorium usually appears as a whitish conical mass, close to the roots of the hosts. Large haustoria have been found attached to other sandal roots (Barber 1905).

Results

Species with haustoria were identified as: *Casuarina glauca, Acacia aneura* (Queensland mulga), *Ehrarta calycina* (South African veldt grass) in Manning Road Bed; *Acacia saligna* in Bed 6A; *Acacia aneura, S. spicatum, S. album* in Bed 6; *Acacia saligna, A. aneura, S. album* in Bed 1A; *A. aneura, S. spicatum* in Bed 3 and Bed 7; *A. aneura, S. spicatum* and *Gompholobium tomentosum* in Bed 9 and *Acacia rhodophloia, S. spicatum, S. album* in Bed 10. Haustoria development varies between hosts (Table 36).

Eight species of plants that were identified as hosts of *S. album* in 8 different beds were then classified into 2 categories. The first has at least 10 haustoria visible along a root section of 50 cm exposed by digging. The first had a high number of haustoria (+++++: >20; ++++: 16-20; +++: 11-15). All plants in this group were then classed as in a healthy state, in poor health or as dead (Table 36). It was found that healthy plants were *C. glauca, Ehrarta calycina, A. saligna, A. rhodophloia*, and *G. tomentosum*. The second category had fewer than 10 haustoria (++: 6-10; +: <6). Of this category, only one species was found dead in 3 beds (Manning Road bed, bed 3 and bed 7), that was *A. aneura* (Queensland mulga). *A. aneura* in other beds (1A, 6, and 9) was in poor health but not dead. Observations revealed some haustoria were attached between *S. album* and neighbours of the same species, and *S. album* with *S. spicatum* (especially in Beds 6, 1A, 3, 7, 9 and 10).

Table 36. Identification of hosts and scoring of haustoria development associated with *S. album* in the FTA.

Location (Beds)	*S. album* tree no.	Host	Host condition	Haustoria development
Manning Road	36	*Casuarina glauca*	Alive (good)	++++
		Acacia aneura	Dead	+
		Ehrarta calycina	Alive (good)	+++
Bed 6A	8	*Acacia saligna*	Alive (good)	+++++
Bed 6	19	*A. aneura*	Alive (poor)	+
		Santalum spicatum	Alive (good)	++
		S. album	Alive (good)	+
Bed 1A	19	*A. saligna*	Alive (good)	+++++
		A. aneura	Alive (poor)	+
		S. album	Alive (good)	+
Bed 3	9	*A. aneura*	Dead	+
		S. spicatum	Alive (good)	++
Bed 7	8	*A. aneura*	Dead	+
		S. spicatum	Alive (good)	++
Bed 9	3	*A. aneura*	Alive (poor)	+
		S. spicatum	Alive (good)	++
		Gompholobium tomentosum	Alive (good)	++++
Bed 10	25	*A. rhodophloia*	Alive (good)	+++
		S. spicatum	Alive (good)	++
		S. album	Alive (good)	+

+++++, ++++. +++ : high number of haustoria; +, ++ : small number of haustoria

Additional observations on different *S. album* trees were conducted at the same time (September 1998) by Joy Jones (undergraduate student). She found four species of plants developed haustoria in association with *S. album*. These were *A. acuminata, A. saligna, Hardenbergia comptoniana* and *A. aneura*. Two of these species were in poor health: the jam tree *A. acuminata* and the Queensland mulga *A. aneura*. Plants of the other two species (*Hardenbergia comptoniana* and *A. saligna)* were in good health. These two species were found with several haustoria attached to *S. album*.

Several *Citrus* trees were located in the Field Trial Area (Bed 6A, Bed 6, Bed 3 and Bed 1A) about 9 to 10 years ago. Several reached 2 to 3 m in height. When the *S. album* trees were planted at that area, most of the *Citrus* trees were dead within 2 to 3 years. Those that survived beyond this period were located further away (4 to 5 m) from the *S. album* trees than the others, but only survived 2 to 4 more years before dying (Peter Mioduszewski, FTA staff 1999).

Discussion

It is assumed that plants frequently found with sandalwood include 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 parasitism that can be tolerated by particular host communities. Species known to be excellent hosts in Western Australia of *S. spicatum* are the jam tree *A. acuminata* and the mulga *A. aneura*. The hosts that were used in the FTA were similar with only one or two species in each bed. The balance between competitive and host effects is related to growth conditions (Watkinson and Gibson 1988). *A. acuminata* is in poor condition near a number of sandalwood occurences at FTA and also in the wheat belt. Another favoured species, *A. tetragonophylla* (Loneragan 1990) is present, but now scarce, near some sandalwoods at Sandford Rock Nature Reserve (SRNR) and it may have declined due to sandalwood (Fox, 1997). On the other hand, *Allocasuarina huegeliana* appears to be more robust than the *Acacia* species; it reaches a larger size and probably persists longer. It may not suffer as much from parasitism as *A. acuminata* and *Citrus* trees at the FTA.

Plant species that were found to be hosts of *S. album* were mainly trees and only 6 of 8 host species indentified were in a healthy state. The 6 healthy species are *Casuarina glauca, Ehrarta calycina, A. saligna, A. rhodophloia, Gompholobium tomentosum,* and *Hardenbergia comptoniana.* Five species had high scores for haustoria development (*C. glauca, A. saligna, G. tomentosum, A. rhodophloia* and *H. comptoniana*). Haustoria development by *S. album* was also found on *S. album* and *S. spicatum*. As a hemi-parasitic species, *S. album* can parasitize over 300 species from grasses, other herbaceous plants to other sandalwood plants. Under gregarious conditions, self-parasitism is common. *S. album* establishes haustorial connections with the host plants for its requirement (Barber 1905, Applegate *et al.* 1990, Rai 1990).

It is suggested that haustorial connection between grasses and sandalwood might enhance N status and relieve water storage. Association between grass, understorey shrubs and sandalwood has been recorded in Vanuatu, Cook Islands, India and Western Australia (Sykes 1980, Applegate *et al.* 1990). Some researchers suggest that establishment of sandalwoods in mixed vegetation, allowing more hosts may provide better stimulation of growth to the parasite (Padmanabha, Nagaveni and Rai 1988).

In Indonesia, sandalwood plants are established in gardens to protect them from weeds (Hamzah 1976). Whereas *S. album* is relatively fast growing and a valuable resource in its own right, best production is likely where it is not considered as part of a conventional agroforestry system, especially if annual crops are involved (Fox *et al.* 1996).

Some parasitised *A. aneura* and *A. acuminata* were found in poor health with a number already dead, apparently killed by *S. album*. These two species have large numbers of haustorial development in association with *S. album* lateral roots. Sandalwood species have extensive lateral roots, that may run for 25 to 30 m from the tree. Along the whole length of the lateral roots, fine feeder roots develop haustoria which have the potential to parasitise suitable host roots (Herbert 1925).

Some research has been done to describe the relationship between sandalwood plants and their hosts (Crossland 1982, Barrett, Wijesuriya and Fox 1985, Hirano 1990). In the field, sandalwood plants appear to react well to fertilizer and are apparently able to obtain at least some part of the nutrient requirement directly from the soil (Nasi 1995). It is of interest that many species parasitized by sandalwood are nitrogen fixing (Neil 1990). Solutes transferred from hosts include N, Na, K, P, water and amino acids (Lamont 1985; Fox *et al.* 1995 b). The function of sandalwood haustoria may include major sites of synthesis and export of proline, and haustoria may have a role in osmotic adjustment in aquiring water from hosts under differing levels of stress (Tennakoon and Pate 1998).

Sandalwood plants are capable of photosynthesis but require some nutrients from the hosts to survive. K, Ca, N, Cu are transferred from *A. acuminata* to sandalwood (Struthers *et al.* 1986). The examples of poor health and death of some *Acacia* in association with *S. album* at Curtin FTA, indicate that *S. album* diminishes host survival. Only a few species of plants were available as long-term hosts in the Curtin FTA. The relatively poor health, especially poor crowns, of *A. acuminata* compared with the same species growing in absence of *S. spicatum*, suggest that it is damaged by the parasite. Measurement of the concentrations of nutrients by sampling of two *A. acuminata* hosts and the hemi-parasitic mistletoe *Amyema preissii* during three seasons of the year, indicated that Cu, Zn, Mg, Na and K were higher in the mistletoe than in the host. There was no trend of Ca and N, but Fe was higher in the host than mistletoe (Lamont and Southall 1982).

In New Caledonia, the concentrations of mineral needs and tolerances of sandalwood (*S. austrocaledonicum*) differ between companion species on the same substrates. Comparison of the foliar mineral composition of sandalwood and of *Acacia spirorbis* indicates that, except for nitrogen, particularly high in *A. spirorbis* (Leguminosae), the major mineral elements are more abundant in the sandalwood (Veillon and Jaffre' 1995).

Self-parasitism observed in this study has been described in India (Barber 1905). The hemi-parasitic plants form contacts with a variety of hosts but fully differentiated haustoria are confined to woody roots (Simpson and Fineran 1970; Applegate *et al.* 1990; Rai 1990). The largest size of haustorium has been found in examples of self-parasitism (Barber 1905). Haustoria commence as whitish limpet-like bodies. From hemispherical, they become elongated, through growth in length of the host root. Elongation takes place at right angles to the length of the root attacked, keeping pace with secondary thickening. The mature haustorium shape may be generally described as a flattened cone or bell drawn out laterally on two sides. The area of attachment and the scar left behind by the haustorium are oval, and the contact surface is concave, fitting closely to the bark of the host.

Death of *Citrus* trees at the FTA is associated with *S. album* parasitism. Barrett and Fox (1997) report that concentrations of minerals in *S. album* seedlings are higher than in trees. Concentrations are higher than in *Nuytsia floribunda* (Hocking 1980), another parasitic tree. Concentrations are higher than: *Citrus* spp, *Prunus* spp, and mango (Reuter and Robinson 1986) and also mature leaves, stem and root from parasitic *S. spicatum* (Struthers *et al.*, 1986).

Conclusion

A range of hosts of *S. album* was found with only six species of plants being classed as being able to cope with the stress of being parasitised by *S. album* in the Curtin

FTA. These host plant species were *Acacia saligna, Casuarina glauca, Gompholobium tomentosum, Acacia rhodophloia, Ehrarta calycina* and *Hardenbergia comptoniana.* As these six species were healthy, they could be good medium to long-term hosts for *S. album.* The range of hosts for *S. album* might have been greater if more species had been present.

Less suitable species in the long-term are *A. acuminata* (the jam tree) and *A. aneura* (Queensland mulga variety). Both were in poor health condition and some had died by the time of observation. *Citrus* trees are also unsuitable medium term hosts for *S. album* as they are killed within several years of the *S. album* attaching itself to the tree. *S. album* diminishes hosts, especially *A. acuminata, A. aneura* and *Citrus* trees. It is also concluded that *A. acuminata. A. aneura* and *Citrus* trees would not be good hosts for a long-term parasitic relationship.

Indian sandalwood can self-parasite with both itself and with individuals of *S. spicatum.* The limitation of nutrient concentrations as resources in the soil might stimulate the connection of younger sandal roots to older sandal roots.

7. General Conclusion

Four experiments have been conducted in the nursery stage to investigate aspects of early growth and host relationships in Indian sandalwood *S. album* from September 1998 to September 1999. Results of these experiments can be considered as appropriate to the experimental objectives as below:

Germination

Three batches of *S. album* seed from three sources (Bangalore, Kununurra and FTA) differed in germination ability. Laboratory testing suggested that, in addition to differences in seed sources (parent trees) and also in conditions (climate), batches were affected by the length of storage and by treatments applied at collection and conditions of storage. Germination results of these three seed batches indicated that larger seed had greater germination percentage than medium and small seeds. The length of time in days for the first germination were different: the medium-weight seeds took 29 days, the heaviest seeds took at least 44 days and the smallest seeds took at least 98 days. Total days for final germination were also different: heaviest seeds required 148 days; the medium seeds 126 days; and the small seeds 117 days. It is suggested that more experimentation is needed to confirm that seed size within batches make significant contributions to the potential for renewal within populations of *Santalum album*.

Relationship between *S. album* and hosts

Hosts affect seedling growth rate in *Santalum album* by as early as 28 days after planting together. *Alternanthera* sp. as a single pot-host promotes *S. album* growth better than *Acacia acuminata* and *Citrus* rootstock. It can be concluded that *Alternanthera* sp. is the superior pot-host for *S. album*. The use of combinations of pot-hosts suggests that using *Alternanthera* sp. and *Citrus* rootstock together allows enhanced contributions to growth rate of *S. album* in terms of height, haustoria development and dry weight. It is concluded that combinations of hosts can provide better nutrition than that provided by a single host. Also, it can be said that *Alternanthera* sp and *Citrus* rootstock are preferentially parasitised by *S. album*. Comparison of dry weights of plants at harvest time indicates that *S. album* diminished hosts.

S. album and _Alternanthera_ sp.

Indian sandalwood, *S. album,* is able to take up supplementary nutrient solutes via its leaf system. It can survive in the sterile medium used without a host, for at least 3 months. However, plants so exposed suffer during this period. Omission of all nutrients or treatments lacking individual nutrients, effect leaf fall and premature death of *S. album* seedlings. Application of N, P, K and trace elements as supplementary supply promotes total leaf number. Comparison of sets with and without *Alternanthera* sp. as hosts for all treatments suggests that in absence of *Alternanthera* sp., supplementary nutrient solutes do not promote enhanced growth of *S. album* seedlings. It can be concluded that *S. album* seedlings depend on *Alternanthera* sp. for some essential nutrients to maintain growth and survival. In other words, certain minerals are probably transferred from hosts to sandalwood, and these are likely include both major and minor nutrients.

Potential hosts of _S. album_

A range of *S. album* in cultivation at Bentley was found with only six species of plants being classed as being able to cope with the long-term stress of being parasitised. These six plant species, by virtue of their relatively healthy condition, can be said to be good hosts for *S. album* in a long-term host parasite relationship. The range of hosts for *S. album* might be more if more species had been present. The six species of plants documented were *Acacia saligna, Casuarina glauca, Gompholobium tomentosum, Acacia rhodophloia, Ehrarta calycina* and *Hardenbergia comptoniana*. Two other species are considered to be good hosts: *A. acuminata,* the jam tree, and *A. aneura,* particularly the Queensland mulga variety. Both were in poor health condition and some of them were dead at the time of observation. *Citrus* trees are also unsuitable hosts for *S. album* as they are killed within several years of the *S. album* attaching itself to the tree. From these observations it can be said that *S. album* diminishes hosts. It is also concluded that *A. acuminata; A. aneura* and *Citrus* trees may not be good hosts for a long-term parasite relationship with *S. album.*. This investigation also found that Indian sandalwood will parasitize itself and *S. spicatum.*

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Appendix 1. Days to germination and total number of *S. album* germinants for seed from 3 sources.

Day	Number of germinations			Cumulative germination			Cumulative percentage		
	Bangalore n=400	CALM n=1500	FTA n=100	Bangalore n=400	CALM n=1500	FTA n=100	Bangalore n=400	CALM n=1500	FTA n=100
1	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0
24	3	1	0	3	1	0	0.75	0.07	0.00
25	0	2	0	3	3	0	0.75	0.2	0.00
26	1	2	0	4	5	0	1.00	0.3	0.00
27	2	0	0	6	5	0	1.50	0.3	0.00
28	0	4	0	6	9	0	1.50	0.6	0.00
29	4	2	0	10	11	0	2.50	0.7	0.00
30	4	1	0	14	12	0	3.50	0.8	0.00
31	0	1	0	14	13	0	3.50	0.87	0.00
32	0	0	0	14	13	0	3.50	0.87	0.00
33	3	10	1	17	23	1	4.25	1.53	1.00
34	0	0	0	17	23	1	4.25	1.53	1.00
35	2	2	0	19	25	1	4.75	1.67	1.00
36	0	0	0	19	25	1	4.75	1.67	1.00
37	1	0	0	20	25	1	5.00	1.67	1.00
38	0	0	0	20	25	1	5.00	1.67	1.00
39	1	0	0	21	25	1	5.25	1.67	1.00
40	0	0	0	21	25	1	5.25	1.67	1.00
41	7	10	0	28	35	1	7.00	2.33	1.00
42	1	1	0	29	36	1	7.25	2.4	1.00
43	0	0	0	29	36	1	7.25	2.4	1.00
44	0	2	1	29	38	2	7.25	2.53	2.00
45	1	2	1	30	40	3	7.50	2.67	3.00
46	0	0	0	30	40	3	7.50	2.67	3.00
47	0	0	0	30	40	3	7.50	2.67	3.00
48	4	4	1	34	44	4	8.50	2.93	4.00
49	0	0	0	34	44	4	8.50	2.93	4.00
50	3	3	0	37	47	4	9.25	3.13	4.00
51	0	0	0	37	47	4	9.25	3.13	4.00
52	1	2	1	38	49	5	9.50	3.27	5.00
53	2	3	0	40	52	5	10.00	3.47	5.00
54	0	0	0	40	52	5	10.00	3.47	5.00
55	1	3	0	41	55	5	10.25	3.67	5.00

Appendix 1 (continued)

Day	Number of germinations Bangalore n=400	CALM n=1500	FTA n=100	Cumulative germination Bangalore n=400	CALM n=1500	FTA n=100	Cumulative percentage Bangalore n=400	CALM n=1500	FTA n=100
56	0	0	0	41	55	5	10.25	3.67	5.00
57	3	2	1	44	57	6	11.00	3.8	6.00
58	2	3	0	46	60	6	11.50	4.00	6.00
59	0	0	0	46	60	6	11.50	4.00	6.00
60	0	0	0	46	60	6	11.50	4.00	6.00
61	0	0	0	46	60	6	11.50	4.00	6.00
62	0	4	1	46	64	7	11.50	4.27	7.00
63	0	0	0	46	64	7	11.50	4.27	7.00
64	2	3	2	48	67	9	12.00	4.47	9.00
65	0	2	0	48	69	9	12.00	4.60	9.00
66	0	0	0	48	69	9	12.00	4.60	9.00
67	2	1	0	50	70	9	12.50	4.67	9.00
68	0	0	0	50	70	9	12.50	4.67	9.00
69	0	0	0	50	70	9	12.50	4.67	9.00
70	0	2	0	50	72	9	12.50	4.8	9.00
71	0	0	0	50	72	9	12.50	4.8	9.00
72	0	0	0	50	72	9	12.50	4.8	9.00
73	0	0	0	50	72	9	12.50	4.8	9.00
74	0	0	0	50	72	9	12.50	4.8	9.00
75	0	5	0	50	77	9	12.50	5.13	9.00
76	1	0	0	51	77	9	12.75	5.13	9.00
77	1	0	0	52	77	9	13.00	5.13	9.00
78	0	0	0	52	77	9	13.00	5.13	9.00
79	1	2	0	53	79	9	13.25	5.27	9.00
80	1	1	0	54	80	9	13.50	5.33	9.00
81	0	2	0	54	82	9	13.50	5.47	9.00
82	0	0	0	54	82	9	13.50	5.47	9.00
83	0	0	0	54	82	9	13.50	5.47	9.00
84	0	0	0	54	82	9	13.50	5.47	9.00
85	1	1	0	55	83	9	13.75	5.53	9.00
86	2	1	0	57	84	9	14.25	5.6	9.00
87	1	0	0	58	84	9	14.50	5.6	9.00
88	1	0	0	59	84	9	14.75	5.6	9.00
89	0	0	0	59	84	9	14.75	5.6	9.00
90	0	2	0	59	86	9	14.75	5.73	9.00
91	0	0	0	59	86	9	14.75	5.73	9.00
92	0	1	0	59	87	9	14.75	5.8	9.00
93	4	0	0	63	87	9	15.75	5.8	9.00
94	0	0	0	63	87	9	15.75	5.8	9.00
95	0	0	0	63	87	9	15.75	5.8	9.00
96	0	0	0	63	87	9	15.75	5.8	9.00
97	1	2	1	64	89	10	16.00	5.93	10.00
98	0	1		64	90		16.00	6.00	
99	0	0		64	90		16.00	6.00	
100	8	2		72	92		18.00	6.13	
101	1	0		73	92		18.25	6.13	
102	0	2		73	94		18.25	6.27	
103	0	0		73	94		18.25	6.27	
104	0	1		73	95		18.25	6.33	
105	0	0		73	95		18.25	6.33	
106	1	0		74	95		18.50	6.33	
107		0			95			6.33	
108		0			95			6.33	
109		0			95			6.33	
110		0			95			6.33	

Appendix 1 (continued)

Day	Number of germinations			Cumulative germination			Cumulative percentage		
	Bangalore n=400	CALM n=1500	FTA n=100	Bangalore n=400	CALM n=1500	FTA n=100	Bangalore (n=400)	CALM (n=1500)	FTA (n=100)
111		0			95			6.33	
112		0			95			6.33	
113		0			95			6.33	
114		0			95			6.33	
115		0			95			6.33	
116		0			95			6.33	
117		0			95			6.33	
118		0			95			6.33	
119		0			95			6.33	
120		0			95			6.33	
121		0			95			6.33	
122		0			95			6.33	
123		0			95			6.33	
124		0			95			6.33	
125		0			95			6.33	
126		0			95			6.33	
127		0			95			6.33	
128		0			95			6.33	
129		0			95			6.33	
130		0			95			6.33	
131		0			95			6.33	
132		0			95			6.33	
133		0			95			6.33	
134		0			95			6.33	
135		0			95			6.33	
136		0			95			6.33	
137		0			95			6.33	
138		1			96			6.4	
139		0			96			6.4	
140		0			96			6.4	
141		0			96			6.4	
142		0			96			6.4	
143		0			96			6.4	
144		0			96			6.4	
145		0			96			6.4	
146		0			96			6.4	
147		0			96			6.4	
148		0			96			6.4	
149		0			96			6.4	
150		1			97			6.47	

Appendix 2. Four categories of seed weight n=700 seeds from the CALM Kununurra batch.

Seed groups weight (g)	Total seed germination	Total days for germination to occur
< 0.1500	-	-
0.1500 – 0.1749	2	117
0.1750 – 0.1999	8	148
> 0.2000	9	126
Total	**19**	**391**
Mean	**6.33**	**130.33**
SD	3.79	15.95

Appendix 3

Alternanthera **sp.**

Around 80 species from most warmer parts of the world make up this genus of annuals and perennials (and a few aquatics) allied to *Gomphrena*. They are mostly low sprawling or prostrate plants, with weak stems and simple leaves arranged in opposite pairs. Flowers are very small, concealed in dense clusters of chaff-like white or straw-coloured bracts that appear at the leaf nodes. At least one species of *Alternanthera* is used in Asia as a green vegetable and for medicinal purposes. At least 2 species are grown for their colourful summer foliage. Cultivation: Plant in humus-rich, well-drained soil in part-shade or full sun. Propagation is from cuttings or seed in spring.

Alternanthera philoxeroides (Alligator weed).

This South American species is a noxious plant in some warm countries, second only to water hyacinth (*Eichhornia*) among aquatic weeds that cause economic loss.

Acacia **species**

This large genus contains over 1,200 species of trees and shrubs from warm climates. Some are deciduous but most are evergreen. Over 700 are indigenous to Australia. They range from low-growing shrubs to tall trees and many have been introduced to other countries for economic and ornamental purposes. Acacias are also common in tropical and subtropical Africa; most African species are characterised by vicious spines and referred to as "thorn trees". Acacias have either bipinnate leaves or their leaves are replaced by flattened leaf stalks, known as phyllodes, which perform the function of photosynthesis. The tiny flowers, ranging from deep golden yellow to cream or white, and crowded into globular heads or cylindrical spikes, are often fragrant and produce abundant, bee attracting pollen. Fruit are either round or flattened pods. Cultivation: The hard-coated seeds remain viable for up to 30 years. They should be treated by heating and soaking for germination in spring. Some need fire to germinate. In cultivation many species are fast-growing but short-lived (10-15 years). In their native regions they are often disfigured by insect or fungus attack. They do best in full sun and well-drained soil. Some will take part-shade.

***Citrus* rootstock**

The number of original wild species in this genus of evergreen small trees, originally native in Southeast Asian region, is very uncertain as many of the cultivated forms are probably of ancient hybrid origin following their domestication, which took place mainly in China and India. While largely cultivated for their fruit, citrus plants have the bonus of looking attractive in the garden, with glossy evergreen leaves and fragrant flowers. Most species are frost tender to some degree but a few tolerate very light frosts; the lemon is the most cold resistant, especially when grafted onto the related *Poncirus trifoliata* rootstock, and the lime is the least cold resistant, doing best in subtropical locations. All citrus can also be grown in pots, as long as the containers are large and the citrus are grown on dwarfing rootstocks.

Cultivation: Very well-drained, friable, slightly acid, loam soil is best. They need full sun, regular watering and protection from wind, especially during the summer months. Citrus also need regular feeding, including large amounts of nitrogen and potassium for good fruiting. Prune only to remove dead, diseased and crossing wood. Subject to a range of virus diseases, they can be invaded by many pests including scale, leaf miner, bronze orange bug, spined citrus bug and fruit fly. They are rarely propagated by home gardeners as this is done by grafting a specialist task.

Appendix 4. Ranked means in height in 7 treatments (labelled as group) of *S. album* over the trial. Means with an underline in common were not significantly different with the Tukey test at the 0.05 level.

M1.

Tr. 5	Tr. 7	Tr. 4	Tr. 2	Tr. 6	Tr. 3	Tr. 1
2.500	2.847	3.380	3.780	4.127	4.427	5.233

M2.

Tr. 7	Tr. 5	Tr. 4	Tr. 2	Tr. 3	Tr. 6	Tr. 1
3.573	3.700	3.933	4.053	4.740	4.807	5.547

M3

Tr. 4	Tr. 2	Tr. 7	Tr. 5	Tr. 3	Tr. 6	Tr. 1
4.313	4.373	4.520	4.680	5.153	5.553	5.893

M4.

Tr. 4	Tr. 2	Tr. 5	Tr. 7	Tr. 3	Tr. 6	Tr. 1
4.760	4.787	4.913	5.107	5.520	5.980	6.273

M5.

Tr. 4	Tr. 5	Tr. 2	Tr. 3	Tr. 1	Tr. 6	Tr. 7
5.400	5.693	5.940	6.153	6.960	7.107	7. 760

M6.

Tr. 4	Tr. 3	Tr. 1	Tr. 2	Tr. 5	Tr. 6	Tr. 7
6.007	6.607	7.833	8.407	8.407	11.033	12.040

M7.

Tr. 3	Tr. 4	Tr. 1	Tr. 2	Tr. 5	Tr. 7	Tr. 6
7.007	7.447	8.587	13.020	14.660	17.620	18.673

M8.

Tr. 3	Tr. 1	Tr. 4	Tr. 2	Tr. 5	Tr. 7	Tr. 6
8.070	9.470	9.690	19.350	21.040	23.850	27.640

Tr. : Treatment

Appendix 5. Ranked means for total leaf number in 7 treatments of *S. album* over the trial. Means with an underline in common were not significantly different by the Tukey test at the 0.05 level.

M1.

Tr. 5	Tr. 7	Tr. 6	Tr. 4	Tr. 2	Tr. 3	Tr. 1
1.800	2.000	2.533	3.933	4.667	5.200	5.600

M2.

Tr. 5	Tr. 7	Tr. 6	Tr. 4	Tr. 2	Tr. 3	Tr. 1
4.000	4.600	4.600	5.600	6.133	6.267	7.333

M3

Tr. 6	Tr. 4	Tr. 7	Tr. 5	Tr. 2	Tr. 3	Tr. 1
6.267	6.400	6.667	7.067	7.200	7.267	8.200

M4.

Tr. 6	Tr. 4	Tr. 7	Tr. 2	Tr. 3	Tr. 5	Tr. 1
7.067	7.333	7.400	8.067	8.067	8.067	9.267

M5

Tr. 3	Tr. 6	Tr. 4	Tr. 2	Tr. 5	Tr. 1	Tr. 7
9.467	9.533	9.800	10.267	10.400	11.467	11.600

M6

Tr. 3	Tr. 1	Tr. 4	Tr. 2	Tr. 6	Tr. 5	Tr. 7
10.933	11.533	11.600	13.333	14.600	15.067	16.067

M7

Tr. 1	Tr. 3	Tr. 4	Tr. 2	Tr. 6	Tr. 7	Tr. 5
9.530	11.270	12.600	15.330	22.670	23.800	27.330

M8

Tr. 1	Tr. 3	Tr. 4	Tr. 2	Tr. 7	Tr. 6	Tr. 5
11.330	13.330	15.930	22.600	38.130	43.470	48.130

Tr. : Treatment

Appendix 6. Ranked means, for wet weight, dry weight (biomass) and moisture of 7 treatments of *S. album*. Means with an underline in common were not significantly different with the Tukey test at the 0.05 level.

Wet weight

Tr. 1	Tr. 3	Tr. 2	Tr. 4	Tr. 5	Tr. 7	Tr. 6
0.46	0.58	1.92	2.04	7.64	14.8	15.07

Dry weight/biomass

Tr. 1	Tr. 3	Tr. 2	Tr. 4	Tr. 5	Tr. 7	Tr. 6
0.087	0.118	0.436	0.607	2.17	4.36	4.59

Moisture

Tr. 1	Tr. 3	Tr. 4	Tr. 2	Tr. 5	Tr. 7	Tr. 6
0.373	0.462	1.433	1.439	5.37	10.44	10.48

Tr. : Treatment

Appendix 7. Ranked means total number of haustorial development of *S. album*. Means with an underline in common were not significantly different with the Tukey test at the 0.05 level.

Mean total number of haustorial.

Tr. 1	Tr. 3	Tr. 4	Tr. 2	Tr. 5	Tr. 7	Tr. 6
3.00	7.90	12.80	19.70	46.60	59.40	63.50

Tr. : Treatment

Appendix 8. Ranked means height of *Alternanthera* sp. over the trial. Means with an underline in common were not significantly different with the Tukey test at the 0.05 level.

M1	Tr. 7	Tr. 5	Tr. 6	Tr. 2	Tr. 8
	4.593	5.073	6.013	6.587	7.960
M2	Tr. 7	Tr. 5	Tr. 6	Tr. 2	Tr. 8
	5.067	5.440	6.573	6.940	8.167
M3	Tr. 7	Tr. 5	Tr. 6	Tr. 2	Tr. 8
	5.700	6.553	7.233	7.320	8.327
M4	Tr. 7	Tr. 5	Tr. 6	Tr. 2	Tr. 8
	6.447	6.900	7.620	7.747	8.480
M5	Tr. 7	Tr. 5	Tr. 6	Tr. 2	Tr. 8
	7.687	7.847	8.480	9.040	9.947
M6	Tr. 2	Tr. 5	Tr. 7	Tr. 6	Tr. 8
	9.793	10.133	10.567	10.913	10.987
M7	Tr. 5	Tr. 2	Tr. 6	Tr. 8	Tr. 7
	10.313	11.120	11.160	11.913	13.553
M8	Tr. 2	Tr. 8	Tr. 5	Tr. 7	Tr. 6
	14.053	14.667	15.233	16.167	18.460

Tr. : Treatment

Appendix 9. Table 21. Ranked means for total leaf number of *Alternanthera* sp. over the trial. Means with an underline in common were not significantly different with the Tukey test at the 0.05 level.

M1				
Tr. 7	Tr. 6	Tr. 5	Tr. 2	Tr. 8
32.6	47.8	50.8	66.27	73.07
M2				
Tr. 7	Tr. 6	Tr. 5	Tr. 2	Tr. 8
53.87	55.8	58.13	72.07	76.87
M3				
Tr. 6	Tr. 5	Tr. 7	Tr. 2	Tr. 8
66.93	68.2	71.73	83.73	92.53
M4				
Tr. 7	Tr. 5	Tr. 2	Tr. 6	Tr. 8
85.8	92.47	94.67	94.8	117.33
M5				
Tr. 7	Tr. 6	Tr. 5	Tr. 8	Tr. 2
133.93	156.73	179.2	222.87	227.33
M6				
Tr. 7	Tr. 6	Tr. 5	Tr. 2	Tr. 8
149.33	182.33	205.53	246.6	250.53
M7				
Tr. 7	Tr. 6	Tr. 5	Tr. 8	Tr. 2
167.8	212.87	235.27	277.13	288.33
M8				
Tr. 7	Tr. 6	Tr. 5	Tr. 8	Tr. 2
192.67	244.33	269.87	314.00	321.13

Tr. : Treatment

Appendix 10. Ranked means for wet weight, dry weight and moisture of *Alternanthera* sp. Means with an underline in common were not significantly different with the Tukey test at the 0.05 level.

Wet weight

Tr. 7	Tr. 6	Tr. 8	Tr. 5	Tr. 2
109.47	123.81	154.32	162.55	170.23

Tr. 7	Tr. 6	Tr. 8	Tr. 5	Tr. 2
29.920	31.410	43.670	44.770	45.120

Tr. 7	Tr. 6	Tr. 8	Tr. 5	Tr. 2
80.47	92.40	110.65	117.78	125.11

Tr. : Treatment

Appendix 11. Ranked means in height of *A. acuminata* over the trial. Means with an underline in common were not significantly different with the Tukey test at the 0.05 level.

M1:	Tr. 5 1.1	Tr. 7 1.22	Tr. 3 1.4933	Tr. 9 1.5
M2:	Tr. 7 1.5067	Tr. 5 1.5067	Tr. 3 1.75	Tr. 9 1.7667
M3:	Tr. 3 1.9733	Tr. 5 1.9933	Tr. 7 2.02	Tr. 9 2.0467
M4:	Tr. 5 2.1867	Tr. 7 2.26	Tr. 3 2.3867	Tr. 9 2.4667
M5:	Tr. 5 2.747	Tr. 7 2.82	Tr. 3 2.887	Tr. 9 3.520
M6:	Tr. 5 3.26	Tr. 7 3.407	Tr. 3 3.787	Tr. 9 4.433
M7:	Tr. 5 3.553	Tr. 7 4.333	Tr. 3 4.373	Tr. 9 6.427
M8:	Tr. 5 4.493	Tr. 7 6.000	Tr. 9 9.307	Tr. 3 10.853

Tr. : Treatment

Appendix 12. Ranked means for total leaf number in 4 treatments of *A. acuminata* over the trial. Means with an underline in common were not significantly different with the Tukey test at the 0.05 level.

M1:	Tr. 7 3.733	Tr. 3 4.000	Tr. 5 4.333	Tr. 9 4.400
M2:	Tr. 7 4.400	Tr. 3 4.533	Tr. 5 5.267	Tr. 9 4.467
M3:	Tr. 3 5.067	Tr. 7 5.133	Tr. 9 5.733	Tr. 5 5.800
M4:	Tr. 3 5.600	Tr. 7 5.733	Tr. 5 6.133	Tr. 9 6.467
M5:	Tr. 7 6.600	Tr. 5 6.667	Tr. 3 7.667	Tr. 9 7.867
M6:	Tr. 5 6.200	Tr. 7 7.133	Tr. 3 8.933	Tr. 9 9.533
M7:	Tr. 5 6.800	Tr. 7 7.733	Tr. 3 11.067	Tr. 9 12.2
M8:	Tr. 5 7.87	Tr. 7 8.53	Tr. 9 14.87	Tr. 3 18.40

Tr. : Treatment

Appendix 13. Ranked means, for wet weight, dry weight (biomass) and moisture of *Acacia acuminata.* Means with an underline in common were not significantly different with the Tukey test at the 0.05 level.

Wet weight				
	Tr. 5	Tr. 9	Tr. 3	Tr. 7
	0.330	0.990	2.120	5.340
Dry weight/biomass				
	Tr. 5	Tr. 9	Tr. 3	Tr. 7
	0.063	**0.273**	**0.610**	**2.370**
Moisture				
	Tr. 5	Tr. 9	Tr. 3	Tr. 7
	0.267	0.717	1.510	2.970

Tr. : Treatment

Appendix 14. Ranked means in height of *Citrus* rootstock over the trial. Means with an underline in common were not significantly different with the Tukey test at the 0.05 level.

M1			
Tr. 4	Tr. 6	Tr. 7	Tr. 10
12.433	16.867	17.700	20.033
	________	________	
M2			
Tr. 4	Tr. 7	Tr. 6	Tr. 10
18.093	24.767	24.967	31.833
	________	________	
M3			
Tr. 4	Tr. 6	Tr. 7	Tr. 10
20.107	30.2	30.253	34.933
	________	________	
M4			
Tr. 4	Tr. 7	Tr. 6	Tr. 10
22.347	33.947	35.573	39.233
	________	________	
		________	________
M5			
Tr. 4	Tr. 7	Tr. 6	Tr. 10
31.127	41.880	42.673	52.880
	________	________	
M6			
Tr. 4	Tr. 7	Tr. 6	Tr. 10
39.09	57.07	57.59	65.49
	________	________	
M7			
Tr. 4	Tr. 6	Tr. 7	Tr. 10
47.23	65.34	66.51	74.65
	________	________	
M8			
Tr. 4	Tr. 6	Tr. 7	Tr. 10
51.09	67.56	68.55	78.84
	________	________	

Tr. : Treatment

Appendix 15. Ranked means for total leaf number of *Citrus* rootstock over the trial. Means with an underline in common were not significantly different with the Tukey test at the 0.05 level.

M1

Tr. 4	Tr. 10	Tr. 7	Tr. 6
10.4	12.533	17.933	21.133

M2

Tr. 4	Tr. 7	Tr. 10	Tr. 6
19.733	29.6	29.667	30.667

M3

Tr. 4	Tr. 10	Tr. 7	Tr. 6
24.867	31.267	36.2	36.933

M4

Tr. 4	Tr. 10	Tr. 6	Tr. 7
29.87	34.8	40.67	41.47

M5

Tr. 4	Tr. 6	Tr. 7	Tr. 10
44.4	48.0	51.67	51.93

M6

Tr. 4	Tr. 7	Tr. 10	Tr. 6
64.73	70.6	72.73	73.47

M7

Tr. 10	Tr. 7	Tr. 4	Tr. 6
83.27	89.27	91.4	94.2

M8

Tr. 10	Tr. 7	Tr. 6	Tr. 4
91.33	94.8	105.67	112.47

Tr. : Treatment

Appendix 16. Ranked means, for wet weight, dry weight (biomass) and moisture of *Citrus* rootstock. Means with an underline in common were not significantly different with the Tukey test at the 0.05 level.

Wet weight:				
	Tr. 4	Tr. 6	Tr. 7	Tr. 10
	35.95	45.33	46.10	59.43
		________	________	
Dry weight/biomass:				
	Tr. 4	Tr. 6	Tr. 7	Tr. 10
	16.16	20.10	22.44	27.35
		________	________	
Moisture:				
	Tr. 4	Tr. 6	Tr. 7	Tr. 10
	19.79	23.66	25.23	32.08
	________	________		
		________	________	

Tr. : Treatment

Appendix 17. Correlation and Regression Between Harvest Values Experiment 3.

Correlation matrix of mean harvest values for unhosted *Santalum album*

	Leaf area	Root no.	Root area	Haustoria	Mean dry wt
Leaf area	1	NS	**	NS	*
Root no.	0.744	1	*	***	NS
Root area	0.930	0.873	1	*	**
Haustoria	0.681	0.968	0.761	1	NS
Mean dry wt	0.851	0.668	0.899	0.506	1

With n=7 df =5 the correlation coefficient r is as follows
Probability of this value or larger

probability	.1	0.05	0.01	0.001
value	0.6694	0.7545	0.8745	0.9507
symbol	NS	*	**	***

Correlation matrix of mean harvest values for hosted *Santalum album*

	Leaf area	Root no.	Root area	Haustoria	Mean dry wt
Leaf area	1	*	**	**	*
Root no.	0.848	1	*	**	**
Root area	0.894	0.785	1	**	NS
Haustoria	0.875	0.932	0.931	1	*
Mean dry wt	0.807	0.876	0.712	0.792	1

When both sets taken together n=14 df = 12, so levels required are now
Probability of this value or larger:

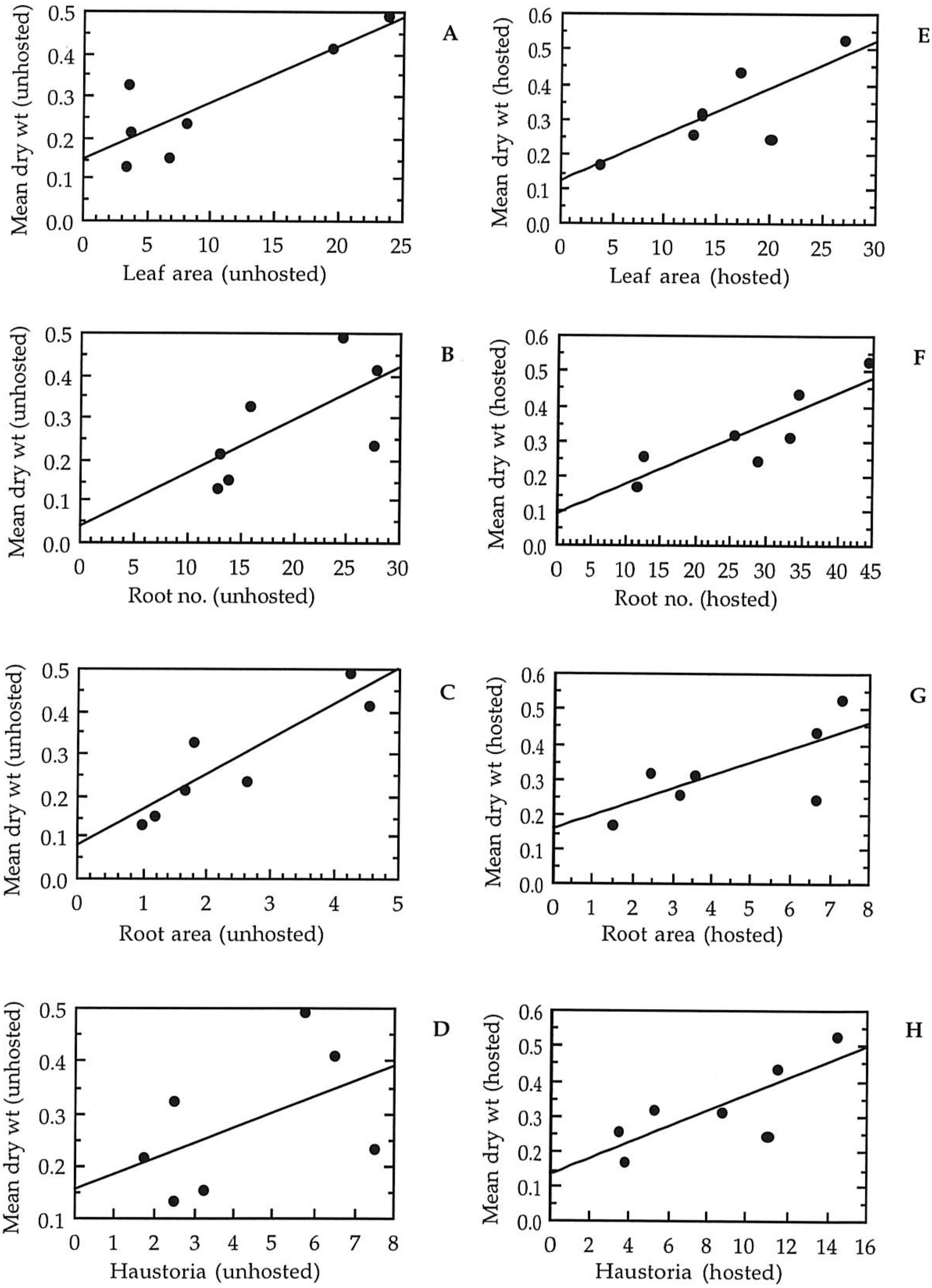
probability	.1	0.05	0.01	0.001
value	0.4575	0.5324	0.6614	0.7800
symbol	NS	*	**	***

Correlation matrix of mean harvest values for hosted + unhosted sets of *Santalum album*

	Leaf area	Root no.	Root area	Haustoria	Mean dry wt
Leaf area	1	***	***	***	***
Root no.	0.796	1	***	***	**
Root area	0.880	0.842	1	***	**
Haustoria	0.781	0.941	0.917	1	*
Mean dry wt	0.828	0.755	0.735	0.632	1

Appendix 17 (continued)

Regression of harvest values for *Santalum album* grown for 20 weeks given various nutrient additions with (right hand side) and without (left hand side) a host of *Alternanthera* cv. to show the dependence of dry weight on other parameters



Appendix 17 (continued)

In Figures A - H above, the Y axis is mean dry weight harvest of *Santalum album*. The values of the coefficient of linear regression are as follows:

Unhosted dry weights				Hosted dry weights			
Figure	X axis	r=	Sig	Figure	X axis	r=	Sig
A	Leaf area (cm^2)	0.851	p 0.05	E	Leaf area (cm^2)	0.807	p 0.05
B	Root number	0.668	p NS	F	Root number	0.875	p 0.01
C	Root area (cm^2)	0.898	p 0.01	G	Root area (cm^2)	0.712	NS
D	Haustoria no.	0.506	p NS	H	Haustoria no.	0.792	0.05

Figures J- M combine unhosted and hosted sets