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TFS Sandalwood Project Prospectus

Competitive effects within and between *Santalum album* and pot host *Alternanthera dentata*

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The growth of Santalum album seedlings and the preferred pot host Alternanthera dentata under nursery conditions is the first important step in establishing this species in plantations. A 19 week pot trial was conducted in a glasshouse at Curtin University of Technology, Perth, Western Australia. The aim was to test whether an increase in host density improved growth of sandalwood seedlings. S. album seedlings had a tendency to grow better at lower densities of A. dentata (one or two hosts per pot), compared with higher densities (three or four hosts per pot). Seedlings with two hosts had greater heights, dry root and shoot weights and leaf area, while seedlings with one pot host had more leaves. There were no clear trends between number of haustorial connections made as host density increased. As host density increased, the leaf area, root and shoot weights of A. dentata declined. Both parasite and host were more affected by competition, however the host was more affected by intraspecific competition, indicated by large competitive responses to each other. S. album seedlings had less effect or response to density of A. dentata after 19 weeks, perhaps due to not being limited by the same resources as the host at this early establishment phase.

Introduction

Successful establishment of *Santalum album* L. in plantations requires the utilisation of appropriate pot hosts under nursery conditions (Radomiljac 1998). Early nursery growth of *S. album* is more rapid and secure when grown with a pot host (Fox 2000). The pot host: parasite relationship continues after plantation establishment and should persist until a second (intermediate) host plant is parasitised (Radomiljac 1998).

Alternanthera is a herbaceous, perennial ornamental shrub and has shown to be an excellent pot host (Fox *et al.* 1996). Various cultivated forms of *Alternanthera* can be planted as cuttings simultaneously with *S. album* (Fox 2000), and this has been adopted in Timor (Fox *et al.* 1995). *A. sessilis* (L.) DC. is known to promote good growth of *S. austrocaledonicum* in New Caledonia (Fox *et al.* 1995). In northern Western Australia, the herbaceous *A. nana* has been reported as an ideal host as it promotes high *S. album* survival and growth following field establishment (Radomiljac, McComb & McGrath 1999).

This paper examines the early growth of *S. album* seedlings with *Alternanthera dentata* (Moench) Scheygr. as a primary host. It specifically aims to determine whether an increase in the density of *A. dentata* improves or reduces early growth (height, leaf numbers, root and shoot mass, number of haustoria and attachments to host roots) of *S. album* seedlings.

Experimental Procedure

Experiments were conducted under a shaded glasshouse in the Field Trial Area at Curtin University of Technology, Perth, W. A. *S. album* seeds were sown in punnets filled with sterilised coarse sand and placed on 25°C heat beds. Moisture was provided five days per week. Germinants were transplanted into rectangular pots (9 x 9 x 15 cm) filled with one part coarse sand: one part fine sand: one part peat, with fertilisers.

Ten randomly selected *S. album* seedlings were grown at four levels of host densities (one, two, three or four per pot). Seedlings were 19-32 days old, between 4-13 cm in height, and had 3-6 leaves. A one-way analysis of variance confirmed no significant difference between *S. album* seedlings (height: $p=0.748$; leaves: $p=0.121$). The host plants used were nine-day-old, rooted *A. dentata* 'Ruby' cuttings which were introduced to seedlings. Seedlings were watered five days per week with rainwater. Pots were placed in a randomised block design and rotated weekly.

Height (cm) and leaf numbers of *S. album* and *A. dentata* seedlings were measured initially and weekly for 19 weeks, from December 2000 to April 2001. An initial harvest of one ran-

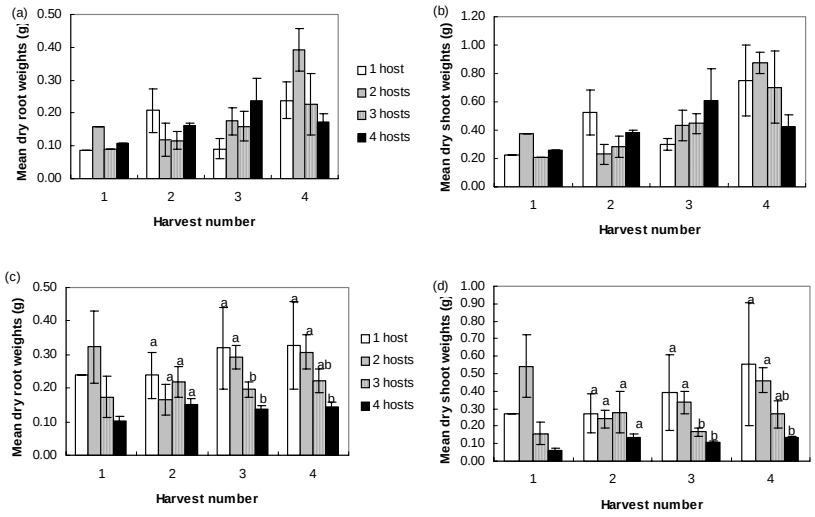

Figure 1. Mean dry root weights of (a) *S. album* and (c) *A. dentata*; and mean dry shoot weights of (b) *S. album* and (d) *A. dentata* at harvest (1=8 wk, 2=12 wk, 3=16 wk and 4=19 wk). SE bars shown. Similar letters indicate no significant differences (a=0.05) using Fisher's LSD test.

domly selected *S. album* (and host) from each treatment was taken at eight weeks. At subsequent harvests, three seedlings were randomly selected at 12, 16 and 19 weeks.

Harvest measurements recorded were:

1. Fresh shoot and root weights (g) of *S. album* and its host.
2. Dry shoot and root weights (72 hr at 60°C) of *S. album* and its host.
3. Leaf area (cm^2) of *S. album* and its host using an electronic planimeter (Otfoto 1.1 and NIH Image 1.62).
4. Number of *S. album* haustoria (at least 0.05 mm).
5. Number of haustorial connections on host roots.

Results

Differences in *S. album* heights were not apparent until after 12 weeks of growth with *A. dentata*. At 19 weeks, seedlings grown with two hosts were the tallest, followed by those growing with one, three and four hosts, with mean heights of 22, 21, 20 and 16 cm respectively. However, there were no significant differences over the whole trial.

Similar trends were observed in the number of *S. album* leaves present at 12 weeks, with seedlings grown at increasing densities of *A. dentata* having a lower mean leaf number, although differences were not significant. At 19 weeks, *S. album* grown with one host had the highest mean leaf number (20), compared with seedlings grown with two, three and four hosts (15-18 leaves).

Initially, there were no clear trends as to whether *S. album* root growth was influenced by the density of its pot host. At 16 weeks, there was a tendency for root growth of *S. album* seedlings to be greater as pot host density increased. However, by 19 weeks, a different trend was observed with *S. album* seedlings growing with two hosts having the best root growth, with a mean dry root weight of 0.39 g (Figure 1a). However, there were no significant differences.

Similar trends were observed in dry shoot weights of *S. album* (also not significant), with seedlings growing with two *A. dentata* hosts having the greatest mean dry shoot weight of 0.87 g, after 19 weeks of growth (Figure 1b). Leaf area of *S. album* seedlings followed the same pattern as dry shoot weights (no significant differences). *S. album* seedlings grown with two pot hosts had the greatest mean leaf area of 88 cm^2 at 19 weeks. In comparison, *S. album* seedlings grown with one, three and four hosts had mean leaf areas of 81, 68 and 44 cm^2 respectively.

Dry root and shoot yield of the pot host *A. dentata* appeared to be more affected by the density at which it was grown compared with *S. album* seedlings. Generally, there was a decrease in mean dry root and shoot weights as density increased. Dry root weights were significantly different at 16 weeks (p=0.001) and 19 weeks (p=0.011), with *A. dentata* grown singly with *S. album* seedlings having the heaviest mean dry root weights of 0.33 g at 19 weeks (Figure 1c). Similarly, there were significant differences in mean dry shoot weights at 16 weeks (p=0.002) and 19 weeks (p=0.012), with *A. dentata* grown singly with *S. album* seedlings having the heaviest mean dry shoot weights of 0.55 g at 19 weeks (Figure 1d).

A. dentata grown at greater densities had lower mean leaf areas, with significant differences present as time progressed at both 16 weeks (p=0.000) and 19 weeks (p=0.025). At 19 weeks, *A. dentata* grown singly had mean leaf area of 48 cm^2, compared with those grown with two, three or four hosts per pot (means of 45, 31 or 17 cm^2 respectively).

Haustoria began to form on roots of *S. album* seedlings grown with two, three and four hosts at eight weeks. At this

Table 1. Mean number of haustoria formed on *S. album* roots and mean number of haustorial connections with roots of *A. dentata* (± SD) at harvest 1= 8 wk (n=1); harvest 2= 12 wk (n=3); harvest 3= 16 wk (n=3); and, harvest 4= 19 wk (n=3). Significance tested using one-way ANOVA (a=0.05) and Fisher's LSD test (similar

	Haustoria numbers				Haustoria connections			
Week	8	12	16	19	8	12	16	19
1 host	0.0	15.3	18.3 c	18.3	0.0	1.7	1.7	4.3
	± 0.0	*± 12.5*	*± 16.3*	*± 18.3*	*± 0.0*	*± 2.9*	*± 2.1*	*± 7.5*
2 hosts	14.0	12.0	50.0 ab	33.7	2.0	0.0	4.0	7.0
	± 0.0	*± 2.6*	*± 8.9*	*± 18.6*	*± 0.0*	*± 0.0*	*± 5.2*	*± 6.1*
3 hosts	3.0	20.7	18.7 bc	22.7	0.0	3.0	5.7	9.7
	± 0.0	*± 2.9*	*± 2.3*	*± 27.2*	*± 0.0*	*± 2.6*	*± 4.0*	*± 10.7*
4 hosts	10.0	14.3	43.3 a	33.7	3.0	2.7	5.3	2.3
	± 0.0	*± 7.5*	*± 14.0*	*± 41.0*	*± 0.0*	*± 2.1*	*± 0.6*	*± 1.5*
F		0.71	5.98	0.235		1.11	0.82	0.58
P		0.574	0.019	0.869		0.401	0.516	0.643

time, only seedlings growing with two and four hosts began to form haustorial connections with the roots of *A. dentata*. By 12 weeks, all seedlings harvested had formed haustoria and haustorial connections. There were no significant differences in the amount of haustoria formed on *S. album* roots, regardless of the number of hosts present. However, at 16 weeks, seedlings growing with two hosts had a significantly higher number of haustoria (mean of 50), compared with those grown with one, three or four hosts (Table 1).

Discussion

A major factor influencing growth and survival of individual plants is competition from neighbours (Firbank & Watkinson 1985). The ability of a species to persist and prosper in a community is often determined by its competitive interactions with other species (Miller & Werner 1987). The growth of *S. album* seedlings was affected by varying densities of its host plant, although these differences were not significant. For the first eight weeks, host plant density had no affect on growth of *S. album.* Between 12 and 16 weeks, growth of *S. album* seedlings was greater as host plant density increased. The effects of competition were evident after 19 weeks, with *S. album* seedlings grown at lower host densities having attained better growth. It was more beneficial to grow *S. album* with two hosts. These provided greater shoot and root biomass, and presumably sufficient resources for greater height and leaf production. Seedlings grown with four hosts appeared to be restricted in growth. This was exaggerated by growth in close proximity and within a small pot environment. It is suggested that a constant increase in the biomass of competitors does not necessarily mean a constant decrease in the amount of limiting resources available to the individual plants. Initially when seedlings first emerge, there may be few competitive interactions. As the individuals grow, they occupy more space and require a greater amount of resources, thus the intensity of competition increases (Miller & Werner 1987).

In *Orobanche crenata,* the number of haustoria formed is affected by the density of host roots in the soil. It is suggested that there may be a positive association between host root weight and parasite weight, due to the increased probability of an attachment forming in a plant with a larger root system. The probability of forming attachments with hosts will differ due to the distribution of host roots in the soil, the susceptibility of the host root to formation of functional haustoria and the presence of host selection mechanisms in the parasite (Graves 1995). However, the increase in density of pot host generally did not influence the numbers of haustoria formed in *S. album* seedlings (except week 16) or number of haustorial connections made with the host.

Distances between individuals and differences in growth form and sizes will strongly influence the competitive effects and responses of species in a plant community (Miller & Werner 1987). Intraspecific competition can cause a reciprocal relationship between mean yield per plant and density (Firbank & Watkinson 1985). In this trial, the host *A. dentata* was more affected by competition within the same species, with significant differences in leaf area, root and shoot biomass at later stages of growth (16 to 19 weeks). Generally, as density increased, biomass of the host plant decreased. Thus, growing *S. album* seedlings with four hosts is not ideal as it not only reduces biomass, but the host plants cannot grow well to support the *S. album* seedlings, due to intraspecific competition.

Throughout the trial, *S. album* seedlings were less affected by competition than the host, *A. dentata.* It is suggested that successful species have either a low response to the abundance of other species and/or such a large effect that the abundance of other species is greatly reduced. Species that have little effect on and response to other species in the community are probably not limited by the same resources and will not be affected by changes in the abundance of other species in the community (Miller & Werner 1987). This could possibly explain the non-significant differences between *S. album* seedlings grown at various host densities. If species have both a large competitive effect on and a large competitive response to one another, the plants are possibly limited by the same resources (Miller & Werner 1987). This was observed between *A. dentata* plants in this trial.

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