COMPETITION BETWEEN VIRGILIA OROBOIDES (BERG.) SALTER, ALBIZIA LOPHANTHA (WILLD.) BENTH. AND ACACIA LONGIFOLIA (ANDR.) WILLD. : A PILOT STUDY.

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ABSTRACT

A pilot autecological study, comparing the indigenous legume tree *Virgilia oroboides*, with two ecologically similar alien legumes, *Albizia lophantha* and *Acacia longifolia* was initiated. Resemblances were found in seed germination biology; with all three species showing extremely rapid germination if the seed dormancy is broken. Differential seed germination inhibition with leaf litter and interspecific seed-mix treatments were recorded, with increasing sensitivity: *Virgilia*, *Albizia* and *Acacia*. A semi-natural 'replacement series' interspecific seedling competition experiment revealed that all three species occupy a similar niche; competition being therefore direct. The order of 'aggressiveness' was found to be *Virgilia*, *Albizia* then *Acacia*; the interaction effects being most clearly registered in the root biomass. Species seed-weights and energies were compared. Also shoot, root increments relative to final shoot, root biomasses were examined, in addition to the performance of each species in nutrient and 'non-nutrient' treated vermiculite. All findings, together with further sundry observations, including in vivo seed, seedling predation measurements, were incorporated into the competition situation. Conclusions were that competitive success of any species combination may vary with a large number of factors, eg. varying nutrient, moisture availabilities of different soils, as well as differential predations on species. It is suggested that if the environment is manipulated correctly, *Virgilia* (or other suitable indigenous species) could be used as a subsidiary control measure against the invasive alien *Albizia* , *Acacia*, etc.

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1. INTRODUCTION

Both *Albizia lophantha* and *Acacia longifolia* represent invasive pest-plants introduced from Australia to the Cape (Stirton, 1978; Taylor, 1978). *Virgilia oroboides*, restricted to the Southern Cape (Coates Palgrave, 1977), probably bears, of all indigenous trees, the closest similarity to *Albizia* and *Acacia* ecologically. Points of resemblance between the species include:-

(1) All grow in moist, relatively fertile south and east mountain slopes with similar altitudinal ranges (Stirton, 1978; Phillips, 1926).

(2) As the species are legumes, nitrogen is presumably fixed by means of root-borne rhizobia. Root nodules can be observed on all three.

(3) They all reproduce from long-lived hard-coated pyrophytic seed alone, and are thus largely dependent on the presence of fire, together with subsequent rains, for en masse establishment from seed reservoirs stored in the soil. It therefore follows that they fulfil similar roles as light-tolerant bush/tree pioneers in the succession sequence.

(4) Unlike most other indigenous trees, *Virgilia* has a very fast growth rate of up to 8 or 12 feet per annum under super-optimal conditions (Phillips, 1926), which is considered to be comparable with the rapid growth rates evident in the introduced *Albizia* and *Acacia*.

Therefore it seems that all three species fill a similar ecological niche. In view of this observation, the broad hypothesis proposed is that:- *Virgilia* could, if environmental conditions are manipulated correctly, be given a competitive advantage over one or both of the two invasive Australian plants.

It was therefore decided to conduct a pilot experimental study on the comparative autecologies of all three species, with particular emphasis on the nature and effects of interspecific interaction.

1.1. Specific aims of the study.

(1) To compare the maximum germination rates and percentages of each species germinated alone, with the rates achieved separately on intra - and interspecific ground-leaf litter mixtures; also the effects of interspecific seed co-germination.

(2) To compare energy contents for seeds of each species, and to correlate the results with short-term, controlled interspecific seedling competition experiments.

(3) To compare the rates of seedling shoot and root growths between species in soil, and for each species grown individually, with and without nutrients, in vermiculite.

(4) To make some observations on the relative seed and seedling predations for each species in nature.

(Seed, hand collected in early summer of the same year, from specific trees in the vicinity of Constantia Nek, Cape Province, was used throughout the study).

2. Maximum seed germination rates and viability percentages alone; on ground-leaf layers and in interspecific mixtures.

2.1. Methods

2.1.1. Preparation of seed germination tests

It is widely accepted that poor germination responses in the three test legume spp. is due principally to the impermeability of the seed coat to water, which prevents absorption of the moisture necessary for the initiation of the germination process. Therefore, all test seeds were individually chipped at their mycropylar ends (care being taken not to damage the embryos). As this procedure also removes the impeding seed coat barrier to the embryo radicle, the fastest possible germination response was ensured.

Three replicate batches of 50 seeds for all species, were each prepared for germination; alone, as well as on finely ground, freshly collected leaf litters from both their own species, and from each of the other test species. In addition, three replicate batches of 0.5/0.5 seed-mix totals of 50 seeds each, using all possible species combinations, were also prepared for testing germination response.

Each seed batch was transferred to a 5 cm petrie dish containing two No. 1 Whatman filter papers. With the "leaf-litter" treatments the filter papers were inserted between 4 g. of freshly ground leaf litter and the seeds. In order to prevent fungal infection, 10 mls. of a mixture of Benomyl (Benlate, Du Pont) and Captan (Captan, Esso), at concentrations of 0.022% and 0.055% active ingredient was added to each dish respectively (as recommended for Acacia germination trials by Clemens, Jones and Gilbert, 1977).

As 27°C has been found optimal for germination response in *Acacia longifolia* (Milton, 1979), the same temperature (± 1°C) was also maintained for incubation of the test series. Humidity was controlled to 100%, and daylength adjusted to a constant 12-hour period at an intensity of 40,000 lux. Adequate moisture conditions were maintained in each dish and counts of germinated seeds (i.e. seed with emerged radicle length greater than 1 mm) were made daily over a period of 14 days. Germinated seeds were not removed for the duration of the test period.

2.1.2. Analysis of data

The mean daily percentage germinations were calculated and subjected to an arc-sine transformation to make them suitable for the analysis of variance (Sokal and Rohlf, 1969). Initially both the rates and final germination percentages for pure seeds of each species were compared with one another visually at the 95% confidence limit. The number of days taken for half the sample to germinate (mean day) was also calculated for each species, together with standard deviations.

Separate comparisons were then made between the arc-sine transformed data for daily germinations of pure seeds, seeds on litter, and seed-mix for each species. As the daily germinations of the treated seeds and the standards (pure seeds) were compared individually, a series of standard t tests were applied to determine whether the differences were significant.

2.2. Results

Germination was quick and decisive. No changes in percentage germination occurred beyond day 7, with the eventual disintegration of ungerminated seeds. It was concluded that this rapid "all or nothing" type of response was probably inspired by the enforced "micropylar-chipping break" in dormancy.

The rates of germination of standard pure seed cultures were similar for all species with percentages which were equal after about the second day (figure 1). The lengths of time taken for half the seeds of each species to

FIGURE 1

GERMINATION RATES OF MICROPYLAR CHIPPED, PLAIN SEED (ALL SPECIES)

(The 95% confidence limits are shown)

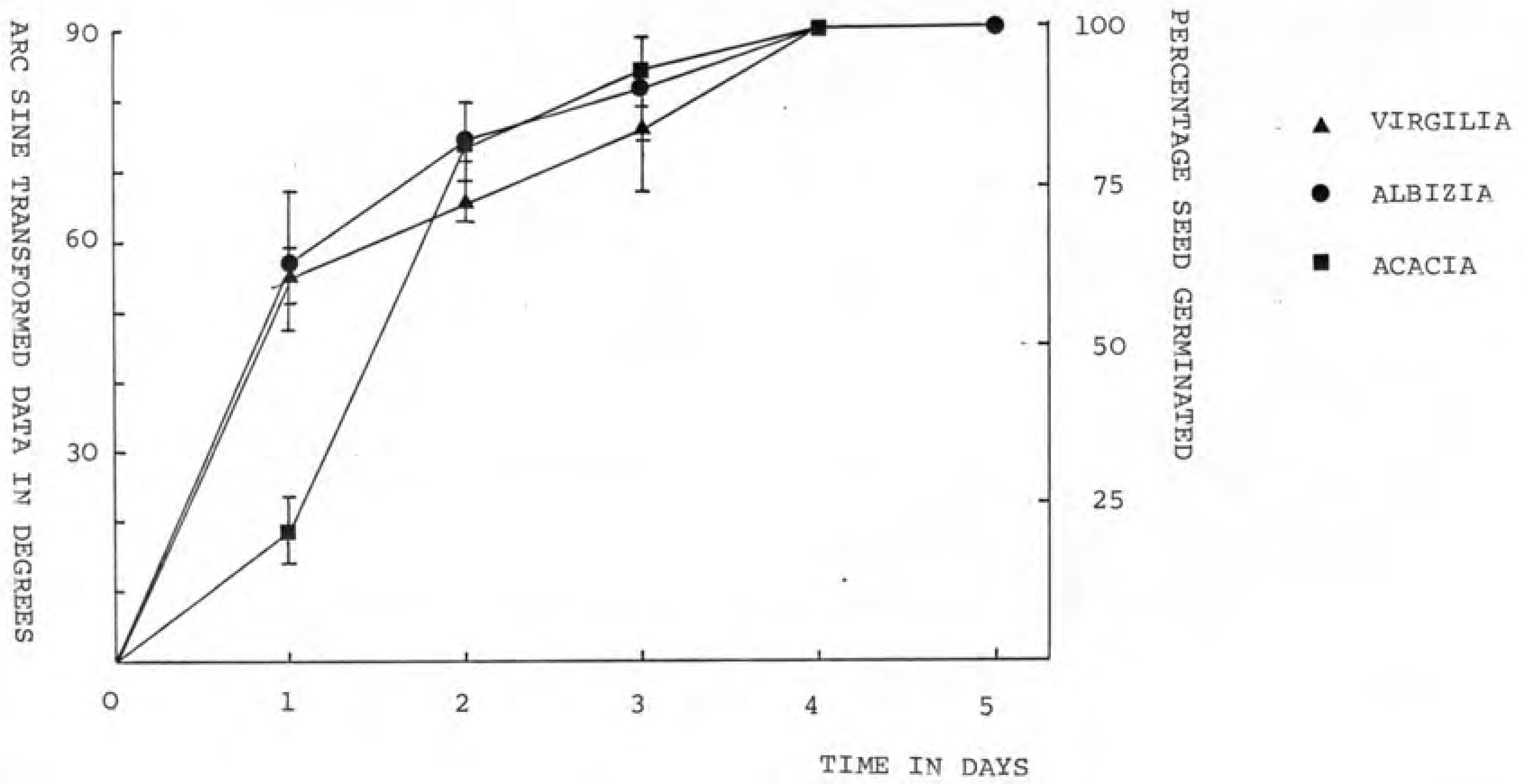


TABLE 1

GERMINATION RATES OF TREATED SEEDS COMPARED WITH PURE STANDARDS - t VALUES

$t^{0.05} = 2.776$

TREATMENT	VIRGILIA SEEDS PLAIN DAYS				ALBIZIA SEEDS PLAIN DAYS				ACACIA SEEDS PLAIN DAYS			
	1	2	3	4	1	2	3	4	1	2	3	4
ON VIRGILIA LITTER	1.01	0.03	0.20	2.02	> 5	> 5	> 5	> 5	3.05	> 5	> 5	> 5
ON ALBIZIA LITTER	> 5	> 5	2.34	1.76	> 5	> 5	> 5	> 5	> 5	> 5	> 5	> 5
ON ACACIA LITTER	4.63	2.69	1.58	1.93	> 5	2.16	3.40	> 5	2.79	> 5	> 5	> 5
WITH VIRGILIA SEEDS	-	-	-	-	3.57	2.83	2.90	1.38	> 5	> 5	> 5	5.34
WITH ALBIZIA SEEDS	1.85	0.75	0.36	2.02	-	-	-	-	1.52	0.26	0.20	0
WITH ACACIA SEEDS	1.47	3.65	0.34	2.01	3.39	0.12	0.32	0.30	-	-	-	-

[ ] INDICATES PERIOD OF INHIBITION

germinate or "mean days" approximated 0.8, 0.8 and 1.5 days for Virgilia, Albizia and Acacia respectively.

Virgilia seeds showed relatively low inhibition of germination in all treatments (Figure 2A). Only on the first and second days, with the Albizia litter treatment, and on the first day, with the Acacia litter, was there a significant reduction of germination rate compared with the pure seed standard (Table 1).

Albizia seeds showed greater sensitivity than Virgilia seeds to the leaf litter and seed-mix treatments (Figure 2B). Inhibition of the germination was most pronounced with the leaf-litter treatments, being greatest overall with its own and with Virgilia leaf-litters, and showed significance from day 3 onwards for the Acacia leaf-litter. The actual rates of germination were significantly reduced in the seed-mix treatments only from days 1 to 3 when mixed with Virgilia seeds and only for day 1 when with Acacia seeds (Table 1).

Of all the species, Acacia exhibited greatest sensitivity to most seed treatments. With the exception of mixture with Albizia seed, all other treatments produced marked inhibition to both the rates, and the overall final germination, of the Acacia seed (Figure 2c, Table 1).

Of interest was the fact that litters of the parent species caused greatest inhibition to the germinations of both Acacia and Albizia but appeared insignificant in connection with Virgilia germination (Figures 2 A, B,C, Table 1).

FIGURE 2

THE EFFECTS OF LEAF LITTER AND SEED-MIX TREATMENTS ON GERMINATION RATES OF MICROPYLAR-CHIPPED SEED (ALL SPECIES)

KEY

○ SPECIES I(J,K) PLAIN
△ SPECIES I(J,K) WITH SEEDS OF SPECIES J(K,I)
□ SPECIES I(J,K) WITH SEEDS OF SPECIES K(I,J)
● SPECIES I(J,K) ON LITTER OF SPECIES I(J,K)
▲ SPECIES I(J,K) ON LITTER OF SPECIES J(K,L)
■ SPECIES I(J,K) ON LITTER OF SPECIES K(I,J)

FIGURE 2A

GERMINATION RATES OF VIRGILIA SEED

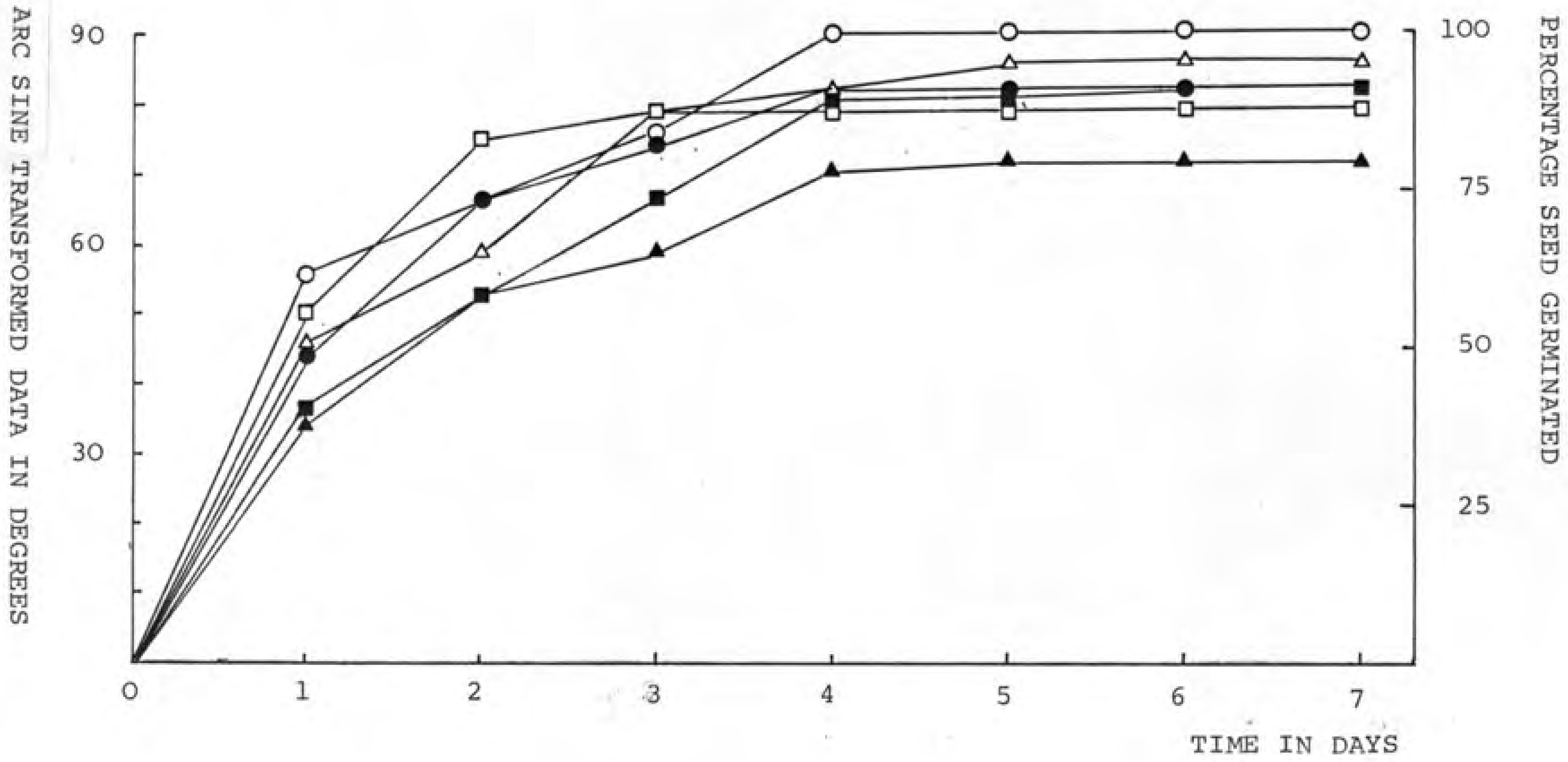


FIGURE 2B

GERMINATION RATES OF ALBIZIA SEED

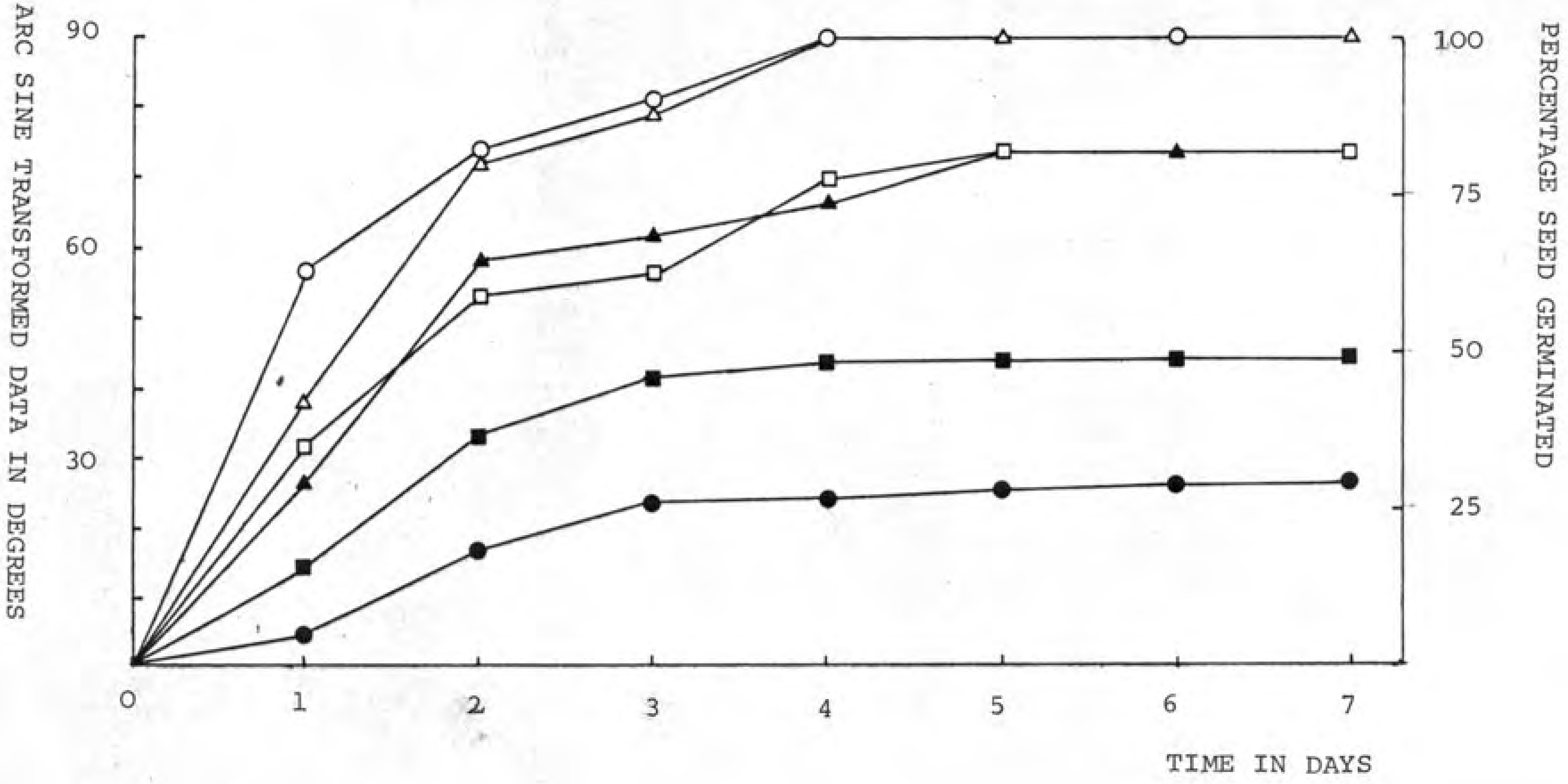
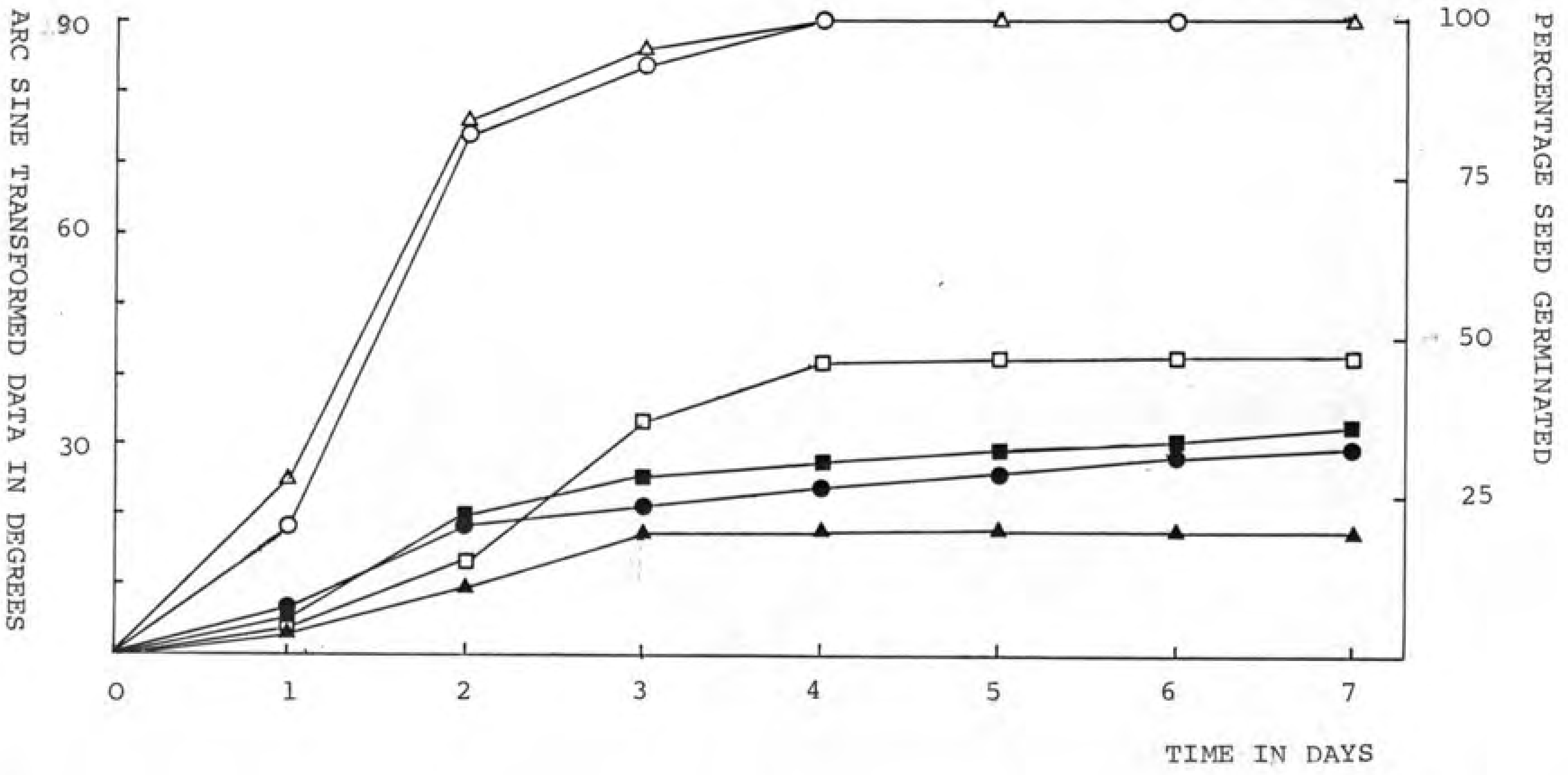


FIGURE 2C

GERMINATION RATES OF ACACIA SEED



3. Controlled early seedling competition.

3.1. Comparative assessment of seed weights and equivalent energies of seeds from each species.

3.1.1. Methods

Random samples of 50 seeds each were selected and all individual seeds weighed in order to make comparisons between species. The samples were dehydrated whole at 65°C, for 7 days, re-weighed, finely ground, and dehydration was continued for a further 3 days. The samples were finally re-weighed to measure the percentage of overall moisture content. It was therefore possible to compare the species resistance to dehydration through the seed-coat with overall percentage moisture.

Two gram sub-samples were then taken from each dry, powdered sample and calorific values were obtained by means of bomb calorimetry, from which the energy contents and their variations, for individual seeds of each species, were calculated.

3.1.2. Analysis of data

Mean fresh seed weights and their standard deviations were obtained and compared for each species. A modified t test for small samples, the Lord's Range test (Sokal and Rohlf, 1969), was then applied to determine the significance of differences in average energy content per seed of each species (obtained as described in Section 3.1.1).

3.1.3 Results

Individual seed weights taken from 50 seeds showed a very low standard deviation; *Albizia* produced the heaviest seeds, followed closely by *Virgilia*, with *Acacia* the smallest (Table 2).

TABLE 2

COMPARISON BETWEEN SEED WEIGHT, SEED MOISTURE CONTENT AND SEED ENERGY FOR VIRGILIA, ALBIZIA AND ACACIA

$L^{0.05} = 1.71$ / $L^{0.01} = 3.96$

SPECIES	WEIGHT OF ONE SEED g	PERCENTAGE MOISTURE LOSS AFTER WHOLE SEED DESSICATION AT 65°C FOR 7 DAYS	TOTAL PERCENTAGE MOISTURE	SUB-SAMPLE BATCH NUMBER	ENERGY PER GRAM OF DRIED SEED KJ	ENERGY PER GRAM OF UNDRIED SEED KJ	ENERGY PER SEED KJ	L VALUES BETWEEN SPECIES FOR SEED ENERGIES
VIRGILIA	0.07858 ± 0.00004	91.31	7.02	1	21.283		1.5550	VIRGILIA vs. ALBIZIA 1.772
				2	21.861		1.5972	
				Mean	21.572	20.057	1.5761	
ALBIZIA	0.09255 ± 0.00005	67.61	7.75	1	20.650		1.7630	ALBIZIA vs. ACACIA 16.449
				2	21.682		1.8511	
				Mean	21.166	19.525	1.8070	
ACACIA	0.016650 ± 0.000007	62.22	8.92	1	18.008		0.2731	ACACIA vs. VIRGILIA 27.553
				2	18.341		0.2781	
				Mean	18.175	16.553	0.2756	

Individual seed energies showed significant differences at $L^{0.05}$ for Albizia and Virgilia, and also at $L^{0.01}$ for Acacia compared with Virgilia and for Acacia compared with Albizia (Table 2). The seed energies/undried seed weight ratios showed the same order of magnitude as the individual undried seed weights. However, the ratio for Acacia was lower than that of both the other species. This means that, relative to the other species, even less energy is present in the Acacia seed than is apparent from the undried weight (Table 2).

Of all the test species, Virgilia, when dehydrated whole, shows the highest percentage of overall moisture content lost through its seed-coat. This possibly indicates a higher seed-coat permeability (Table 2).

TABLE 3

COMPETITION BETWEEN SPECIES AND EFFECTS OF INTERACTION IN MIXTURE: L VALUES

$L^{0.05} = 1.71$
$L^{0.01} = 3.96$

SPECIES PAIR	YIELD MIXED vs ½ YIELD PURE	RELATIVE YIELD TOTAL (RYT)	SPECIES	TOTAL PLANTS RY vs ½ RYT	SHOOTS ALONE RY_s vs ½ RYT_s	ROOTS ALONE RY_r vs ½ RYT_r
VIRGILIA vs ALBIZIA	1.3482	1.0583	VIRGILIA	1.1531	0.6014	5.6933 (S)
			ALBIZIA	2.2288 (S)	0.9954	3.4247 (S)
ALBIZIA vs ACACIA	0.6306	1.0795	ALBIZIA	2.4430 (S)	1.0771	4.0856 (S)
			ACACIA	1.8460 (S)	1.4703	2.7188 (S)
ACACIA vs VIRGILIA	1.5952	0.9882	ACACIA	2.3828 (S)	1.3713	5.3327 (S)
			VIRGILIA	1.2862	0.8429	2.3150 (S)

3.2. Seedling competition using the replacement series technique

3.2.1. Methods

Freshly germinated seed of Virgilia oroboides, Albizia lophantha and Acacia longifolia were sown in pure cultures, as well as in 0.5/0.5 mixtures, with species individuals set alternate to one another, for all species combinations. Fallen seed of Virgilia may be found at natural concentrations of up to 1 seed per 5 cms^2 (Phillips, 1926), whereas that of Acacia can be found at concentrations of up to 3 seeds per cm^2 (Milton, 1979). Since natural concentrations of seed appear high for both these species (and probably also for Albizia), germinated seed were set at concentrations of 1 per centimetre in 7 x 7 matrices (with the omission of plantings at number "49" corners, allowing equal numbers/species). Two replicate matrices were prepared for both pure and mixed cultures. The rich loam soil used for the experiment, was taken from the A horizon at a site in Kirstenbosch National Botanic Gardens, where all three test species are known to occur.

The experiment was run out of doors during late autumn - winter, a cool wet period in the south-western Cape, when field germination of the test species has been observed. Full precautions were taken against any natural predation, and a transparent (95% light transmission) corrugated fibre-glass sheet was suspended 3 feet above the seedling containers in order to permit a controlled, adequate application of moisture.

After twelve weeks the seedlings were harvested, cleaned and then dehydrated in an oven at 80°C. The total dry-weight measurements for shoot and root biomasses were then taken separately for each species, from each culture.

3.2.2. Analysis of data

The "replacement series" approach is an experimental design first introduced by de Wit (1960) to measure the effects, of one species on the other, in species combinations grown in mixtures. This approach adopts as a standard for comparison, the pure stands of each species grown at the same densities as the mixtures, thus allowing for all conclusions to be derived on a proportional and therefore relative basis.

Results are represented pictorially by means of "replacement series" curves for each species combination. In addition, the data were analysed to derive certain important features concerning the species interactions.

Firstly, in order to determine whether or not each test species possesses ecological niche overlap with the others; i.e. whether there is competition for common limiting resource/resources, the "Relative Yield Totals" (RYT) for each of the interacting species pairs were calculated.

The sum of the relative yields of species 'I' grown in mixture with species 'J' (R_I) and of species J grown in mixture with species 'I' (R_J) is equivalent to the RYT for the two species. Here $R_I = \frac{M_I}{P_I}$ and $R_J = \frac{M_J}{P_J}$, where $M_{I(J)}$ = yield of species I(J) in mixture, and $P_{I(J)}$ = yield of species I(J) in pure stand. If the RYT values are equal to unity, it indicates that the mixed species pairs fill the identical ecological 'space' (Harper, 1977).

In order to determine the statistical significance of the conclusions inferred by the RYT values, the <u>actual</u> yield of each mixture was compared with the sum of half the <u>actual</u> yields of the two corresponding pure cultures (Burdon and Pryor, 1975). The 'Lord's Range test' was therefore applied to test whether the species in mixtures were competing for the same ecological niche/resources.

Secondly, whether or not it is found that the species occupy suitably similar ecological niches to allow direct competition for resources, this factor gives no information about the significance of relative enhancement/inhibition effects produced by the mixing. Hence the inferences drawn from the shapes of the 'replacement series' curves (convexity illustrating enhancement and concavity inhibition) were tested. Lord's Range values were thus calculated to see whether the difference was significant between relative yields for the replicate pairs of each species and the corresponding pairs of "expected" relative yields. The "expected" relative yield is defined as being half the value of the calculated RYT for each replicate.

In order to extend the conclusions concerning the effects of the test species interactions, similar "relative yield" analyses were completed for both shoots and roots separately. Actual shoot - root yield borderlines were also depicted on the 'replacement series' diagrams.

3.2.3 Results

All RYT mean values (which are marked on Figures 3A, 4A, 5A) were found to be close to unity, thus providing a rough indication that the test species fill very similar ecological niches to one another.

Comparisons of the actual yields for each mixture with the sum of half the actual yields of the corresponding pure cultures, produced values which were all insignificant at $L^{0.05}$ (Table 3). This means that one must accept the null hypothesis that the species are competing with one another for the same ecological space, which agrees with the conclusions obtained from the RYT values. Inspection of the L values (Table 3) gives an indication of the ecological relationships between the species, as regards competition for the same resource/resources. The order of increasing ecological 'relatedness' appears to be as follows: Virgilia - Acacia, Virgilia - Albizia and lastly, Albizia - Acacia.

The replacement series curves indicate fairly marked enhancement/inhibition effects between the various competing species pairs (Figures 3A, 4A, 5A). The Lord's Range comparisons of the relative yields and ½ RYT's revealed significance at the 95% level for all competitors, with the exception of Virgilia (Table 3). However, it must be emphasized that both Albizia and Acacia show significant inhibition in biomass increment in the presence of Virgilia.

Finally Albizia is significantly enhanced and Acacia significantly

depressed / -

depressed, when in mixture (Table 3).

The comparisons between expected relative yield and observed relative yields, calculated for shoots and roots separately , revealed very definite differences between the respective L values (Table 3). It can clearly be seen that differences in the observed relative yields of shoots alone, for all the species pairs, is insignificant at the 95% confidence level. That most competitive enhancement/inhibition effects are manifest in the root relative yields, is clearly indicated by the much higher L values. Root relative yields show significant differences from the expected values for all species in all combinations with some L values even exceeding the 99% confidence levels: *Virgilia* is enhanced when in mixture with *Albizia*; *Acacia* is inhibited when in mixture with *Virgilia* and *Albizia* is enhanced when in mixture with *Acacia*. Some of the general competition effects for each species are apparent in Figures 3B, 4B and 5B.

In summary, the test species appear to occupy very similar niches, with competition being therefore direct, and with the interaction effects being most clearly registered in the root biomass.

FIGURE 3A

FIGURE 4A

FIGURE 5A

'REPLACEMENT' SERIES DIAGRAMS OF SEEDLING COMPETITION BETWEEN ALL PAIRS OF ALL SPECIES

KEY

▲ VIRGILIA

● ALBIZIA

■ ACACIA

░ SHOOT GROWTH

▤ ROOT GROWTH

FIGURE 3A

A 'REPLACEMENT' SERIES DIAGRAM OF VIRGILIA vs. ALBIZIA

RYT for 0.5/0.5 mixture = 1.056

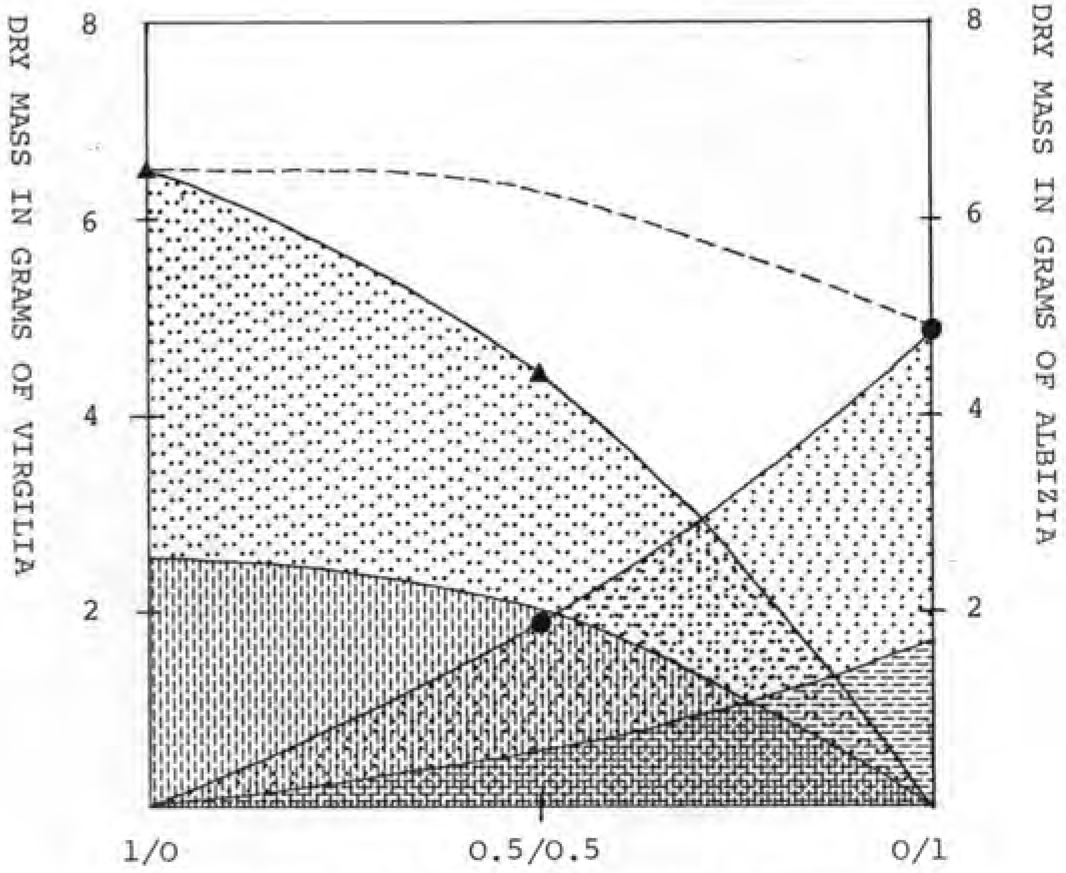
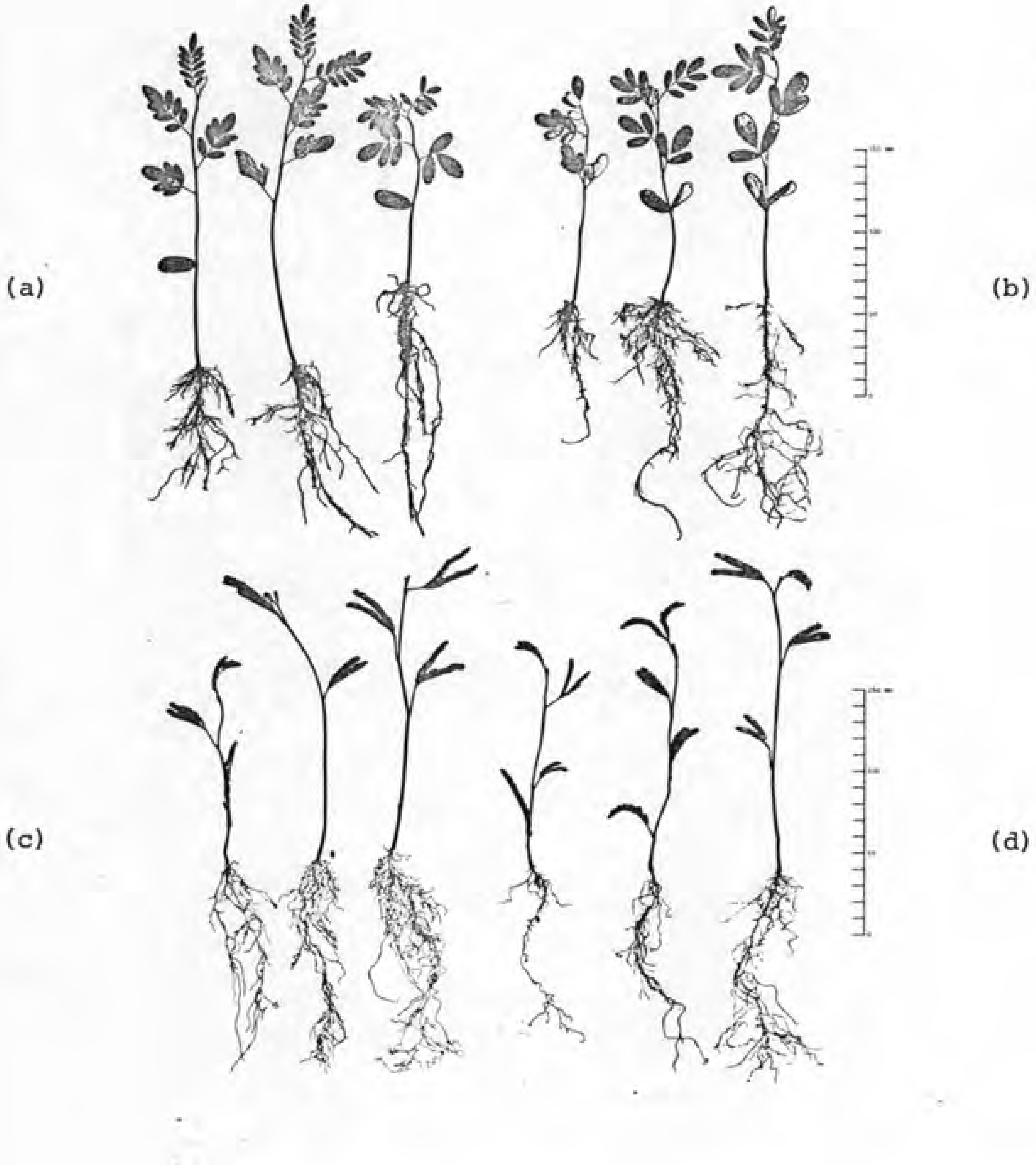


FIGURE 3B

SEEDLINGS SELECTED AT RANDOM FROM PURE AND MIXED STANDS OF VIRGILIA, ALBIZIA - SHOWING EFFECTS OF INTERACTION



(a) 'Pure' Virgilia

(b) 'Mixed' Virgilia - slightly enhanced root development

(c) 'Pure' Albizia

(d) 'Mixed' Albizia - slightly reduced root development

FIGURE 4A

A 'REPLACEMENT' SERIES DIAGRAM OF ALBIZIA vs. ACACIA

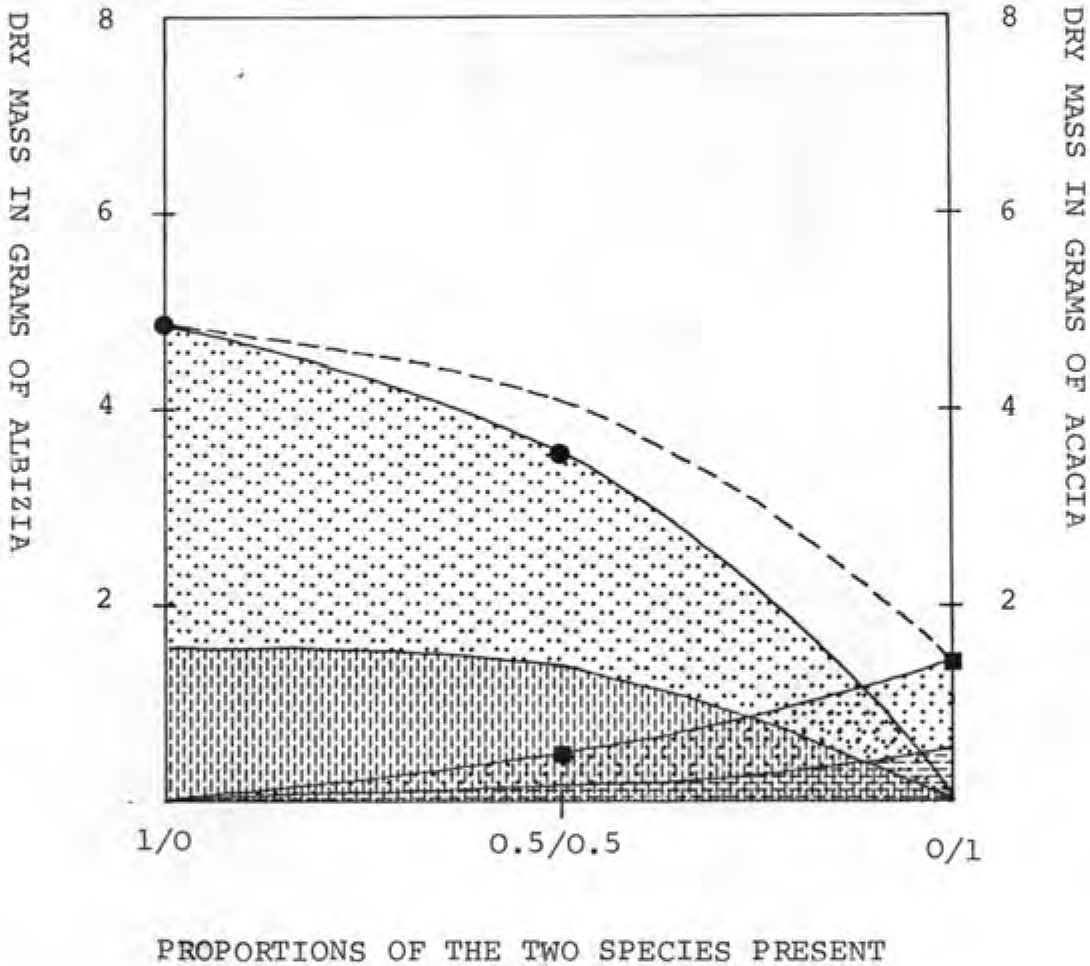
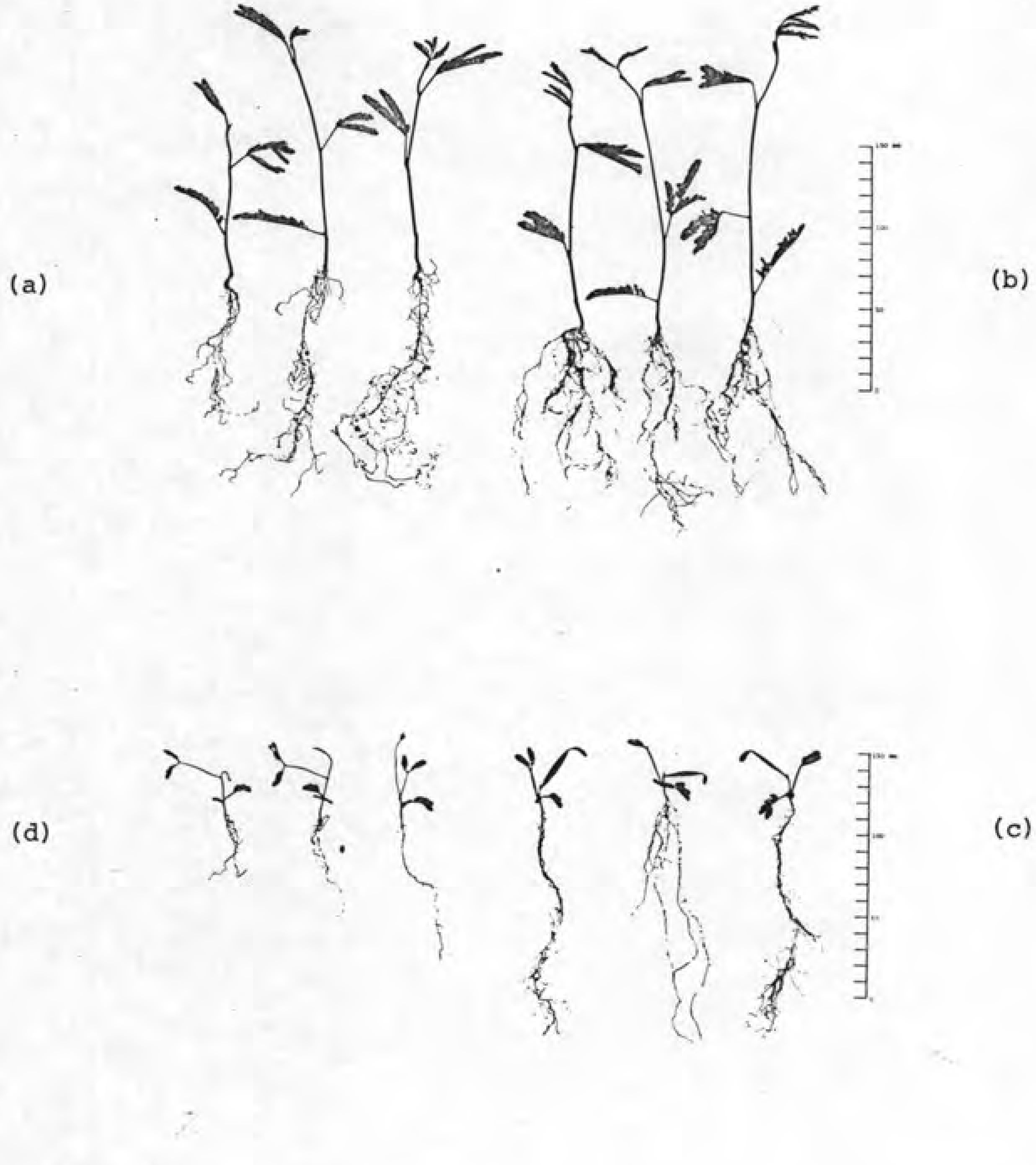

RYT for 0.5/0.5 mixture = 1.082

FIGURE 4B

SEEDLINGS SELECTED AT RANDOM FROM PURE AND MIXED STANDS OF ALBIZIA, ACACIA - SHOWING EFFECTS OF INTERACTION



(a) 'Pure' Albizia

(b) 'Mixed' Albizia - slightly enhanced root development

(c) 'Pure' Acacia

(d) 'Mixed' Acacia - reduced root development and etiolated stems and leaves

FIGURE 5A

A 'REPLACEMENT' SERIES DIAGRAM OF ACACIA vs. VIRGILIA

RYT for 0.5/0.5 mixture = 0.986

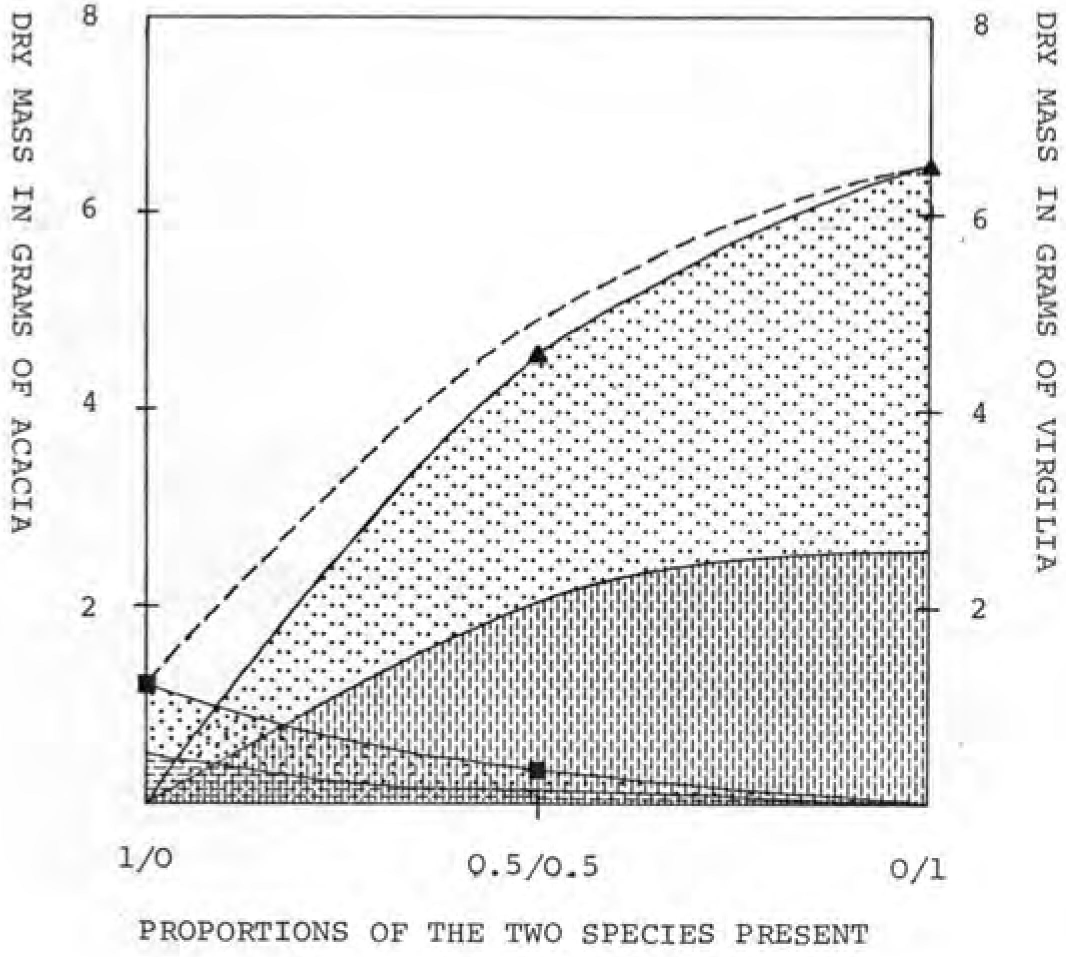


FIGURE 5B

SEEDLINGS SELECTED AT RANDOM FROM PURE AND MIXED STANDS OF ACACIA, VIRGILIA - SHOWING EFFECTS OF INTERACTION

(a) Pure' Acacia

(b) Mixed' Acacia - reduced root development and etiolated stems and leaves

(c) 'Pure' Virgilia

(d) 'Mixed' Virgilia - enhanced root development

4. Early shoot and root growth rates

4.1. A comparison between the shoot and root growth rates of the test spp. grown in soil

4.1.1 Methods

For the purpose of comparing root growth in seedlings of *Virgilia*, *Albizia* and *Acacia*, a set of nine "root chambers" was constructed; applying a principle similar to that used for monitoring relative root growths of sugarcane by Gerard (1978).

In the experiment a single side of each rooting chamber was made out of a transparent perspex sheet, set at a slope of 45° to the vertical, through which changes in root length could be examined at regular intervals. To observe as much of the root growth as possible, each freshly germinated seedling was planted at a distance of 0.5 cm from the edges of the transparent sides of each chamber. Three replicate week-old seedlings for each species were initially planted in individual chambers, and the slanted perspex sides were obscured by means of hinged opaque perspex covers. This prevented inhibition by light of root growth along the transparent surfaces. The soil used and the environmental conditions for growth were the same as those employed in the seedling competition experiment.

Root growth increments, as seen through the transparent perspex, were traced onto detachable transparent plastic sheets, using different colours for each time interval. Markings were made at fortnightly intervals over a period of 6 weeks and after a final longer interval of 3 weeks, thus finally illustrating an overall growth period of 9 weeks (in addition to the 1 week of seed incubation time). The marked root growth increments were later measured by means of an opisometer.

Simultaneous to the marking of root increments, measurements of shoot heights were also taken for each plant.

At the end of 9 weeks, the seedlings were harvested, cleaned and xeroxed in order to determine approximately what proportion of the roots had been visible through the transparent perspex sides of the chambers, while growth was being monitored.

Finally the seedlings were oven dried at 80°C and weighed; roots and shoots separately, for each individual.

4.1.2 Analysis of data

Cumulative shoot and root increments were compared between species for each time interval using a series of one-way Anova variance tests (Sokal and Rohlf, 1969). If the null hypothesis for these tests was rejected, the Tukey's method of multiple comparisons (Zar, 1974) was applied to test significance between individual species combinations. It was thus possible to determine if and when seedlings of each species showed significantly different root and shoot growth rates from one another.

A similar analysis was also performed to test differences between the final mean dry weights for each species.

In addition, certain proportions, together with standard deviations, concerning shoots, roots, were calculated and comparisons made. These were, firstly; final root/shoot length, and root/shoot dry-weight proportions and secondly; final shoot weight/shoot length and root weight/root length proportions.

Results / -

TABLE 4

PERFORMANCE OF SPECIES IN SOIL

4A

COMPARATIVE RATES OF SHOOT AND ROOT GROWTH IN SOIL BETWEEN ALL SPECIES : ANOVA F VALUES AND TUKEY'S RANGES

(i) F OBSERVED VALUES $F^{0.05}_{2,6} = 5.14$

	NUMBER OF WEEKS			
	2	4	6	9
SHOOTS	41.13	41.70	42.92	58.77
ROOTS	51.27	21.06	9.36	5.704

(REJECT Ho THROUGHOUT)

4A (ii) / -

(ii) TUKEY'S RANGE VALUES, = 0.05

(IF CONFIDENCE INTERVAL DOES NOT INCLUDE 0.0 - REJECT Ho (S))

		NUMBER OF WEEKS			
		2	4	6	9
SHOOTS	μ_{vi} vs. μ_{al}	0.84 → 3.36 (S)	0.02 → 3.76 (S)	0.30 → 3.70 (S)	0.44 → 3.76 (S)
	μ_{al} vs. μ_{ac}	0.31 → 2.83 (S)	0.51 → 4.29 (S)	1.27 → 4.67 (S)	2.02 → 5.34 (S)
	μ_{ac} vs. μ_{vi}	2.41 → 4.93 (S)	2.38 → 6.16 (S)	3.27 → 6.67 (S)	4.12 → 7.44 (S)
ROOTS	μ_{vi} vs. μ_{al}	2.37 → 10.43 (S)	11.52 → 45.08 (S)	-0.86 → 112.66 (NS)	-65.31 → 148.51 (NS)
	μ_{al} vs. μ_{ac}	-2.63 → 5.43 (NS)	-12.38 → 21.18 (NS)	-35.06 → 78.46 (NS)	-32.31 → 181.51 (NS)
	μ_{ac} vs. μ_{vi}	3.77 → 11.83 (S)	15.90 → 49.48 (S)	20.84 → 134.46 (S)	9.29 → 223.11 (S)

μ_{vi} = MEAN FOR VIRGILIA

μ_{al} = MEAN FOR ALBIZIA

μ_{ac} = MEAN FOR ACACIA

(i) DRY WEIGHTS IN SOIL AND INTERSPECIFIC COMPARISONS

$$F^{0.05}_{2,6} = 5.14$$

SPECIES	TOTAL DRY WEIGHTS	ANOVA BETWEEN SPECIES F_{OBS}	TUKEY'S CONFIDENCE INTERVALS (IF NOT INCLUDING 0 REJECT Ho(S))
VIRGILIA	.2790	43.6	VIRG. vs. ALB. 0.09 → 0.26 (S)
ALBIZIA	.1018		ALB. vs. ACAC. -0.01 → 0.16 (NS)
ACACIA	.0250		ACAC. vs. VIRG. 0.17 → 0.34 (S)

(ii) SPECIES SHOOT/ROOT PROPORTIONS (WITH STANDARD DEVIATIONS)

SPECIES	ROOT LENGTH / SHOOT LENGTH	ROOT WEIGHT / SHOOT WEIGHT	SHOOT WEIGHT / SHOOT LENGTH	ROOT WEIGHT / ROOT LENGTH
VIRGILIA	22.9 ± 6.2	2.71 ± 0.07	0.0118 ± 0.0010	0.00148 ± 0.00027
ALBIZIA	24.7 ± 3.3	0.873 ± 0.001	0.0132 ± 0.0009	0.00048 ± 0.00007
ACACIA	64.0 ± 21.2	0.68 ± 0.16	0.0305 ± 0.0124	0.00036 ± 0.00008

4.1.3. Results

Visual comparison between the xeroxed seedling roots (Figure 6C) and the transparent sheets whereupon root growth increments had been traced, showed that a considerable part of the root length had been visible during the monitoring procedure.

The analysis comparing rates of shoot increment showed significant difference between species throughout (Table 4A). From the curves in Figure 6(A) it can be noted that the rates of growth for all species appear most rapid over the first two weeks; probably as a result of the initial seed energy "boost". Although *Virgilia* shows a significantly greater shoot length increment than *Albizia* from week 4 onwards, *Albizia* appears to possess a slightly faster rate of growth than *Virgilia*, thus possibly indicating that the former could eventually "overtake" the latter.

A similar situation applies in the case of root growth, in which *Albizia* ceases to show a significantly lower root-length increment than *Virgilia* from week 6 onward (Figure 6B, Table 4A).

Acacia differs from the other species with regard to relative shoot and root growth rates. The *shoot*-length increment from week 2 to week 9 is virtually negligible, unlike the other species, whereas the *root*-length increase is continuous, which is similar in pattern to that of the others (Figures 6A,B).

The dry weights of the harvested plants showed the following order of magnitude: *Virgilia*, *Albizia* and *Acacia*, with no significance in difference between the means of the latter two species (Table 4B).

The proportions of root - / shoot - length increased in the following order: *Virgilia*, *Albizia*, followed by *Acacia* with the highest value (Table 4B). However, root / shoot dry-weight ratios showed the reverse trend.

Further inspection of the data in Table 4B shows that the shoot dry weight/ shoot length values are in the approximate ratio of 15 : 17 : 38 for *Virgilia*, *Albizia*, *Acacia* respectively, indicating a significantly higher value for *Acacia*. However, the corresponding root dry weight / root length ratios, which are 15 : 5 : 4, show that *Virgilia* has emphatically the highest value for this parameter.

Thus it seems clear that both *Albizia* and *Acacia* produce greater lengths of root for less energy than *Virgilia*. Less significant is the fact that *Virgilia* and *Albizia* allocate lower energy per length of stem than *Acacia*.

Some other general observations can be made. Unlike *Virgilia* and *Acacia*, *Albizia* shed its reddish - yellow embryonic seed cotyledons within the first 3 weeks after planting. The cotyledons of *Virgilia* and *Acacia* turned green, hence photosynthetic, soon after germination, and were retained for the full test period (Figure 6C). It was also noted that the *Acacia* seedlings did not develop true 'phyllode' leaves (characteristic of mature plants) during the same period (Figure 6C). (In additional unharvested specimens these became apparent only at about 3 months of age).

FIGURE 6A

'ROOT CHAMBERS' - GROWTH IN SOIL OF SHOOTS (ALL SPECIES)

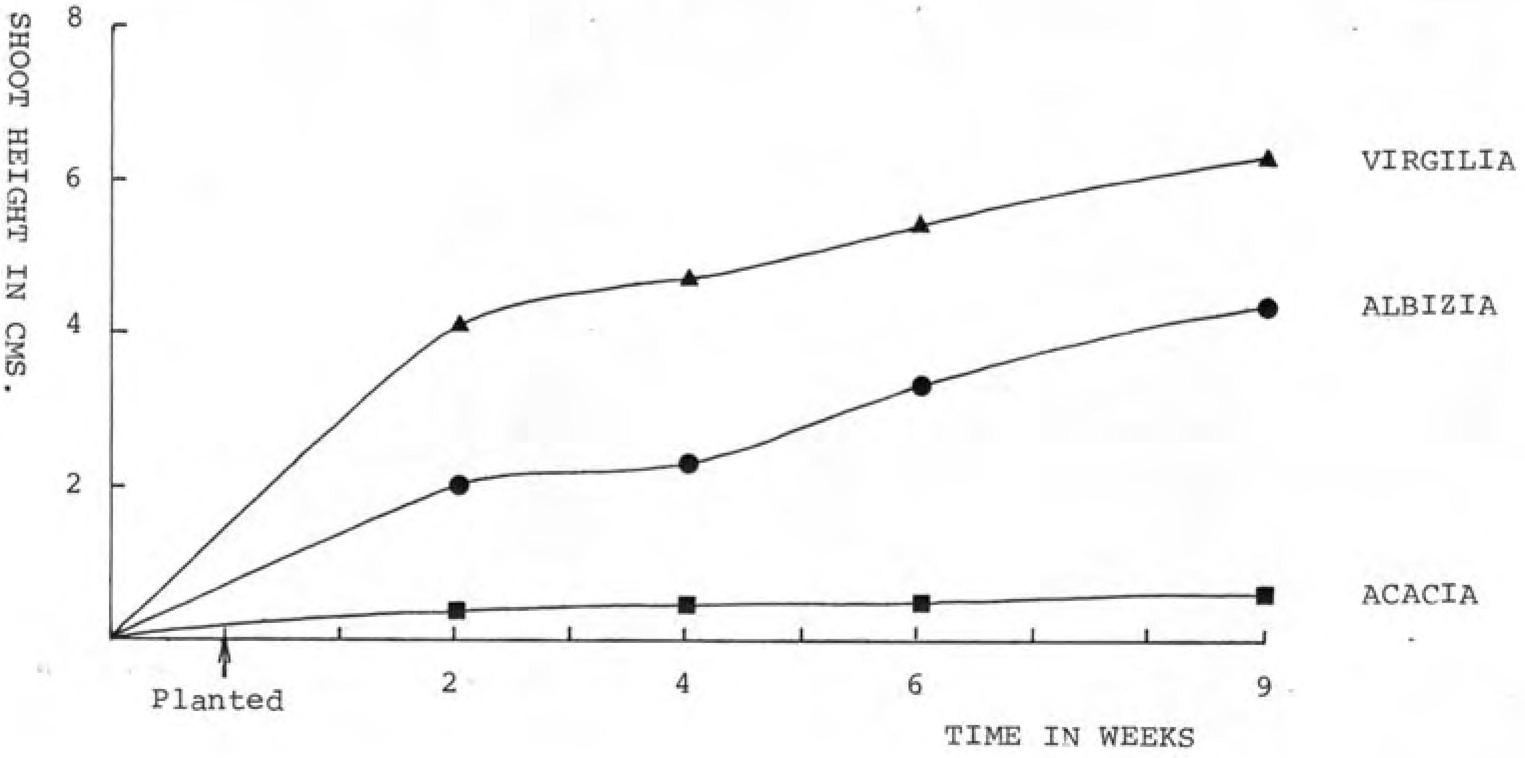


FIGURE 6B

'ROOT CHAMBERS' - GROWTH IN SOIL OF ROOTS (ALL SPECIES)

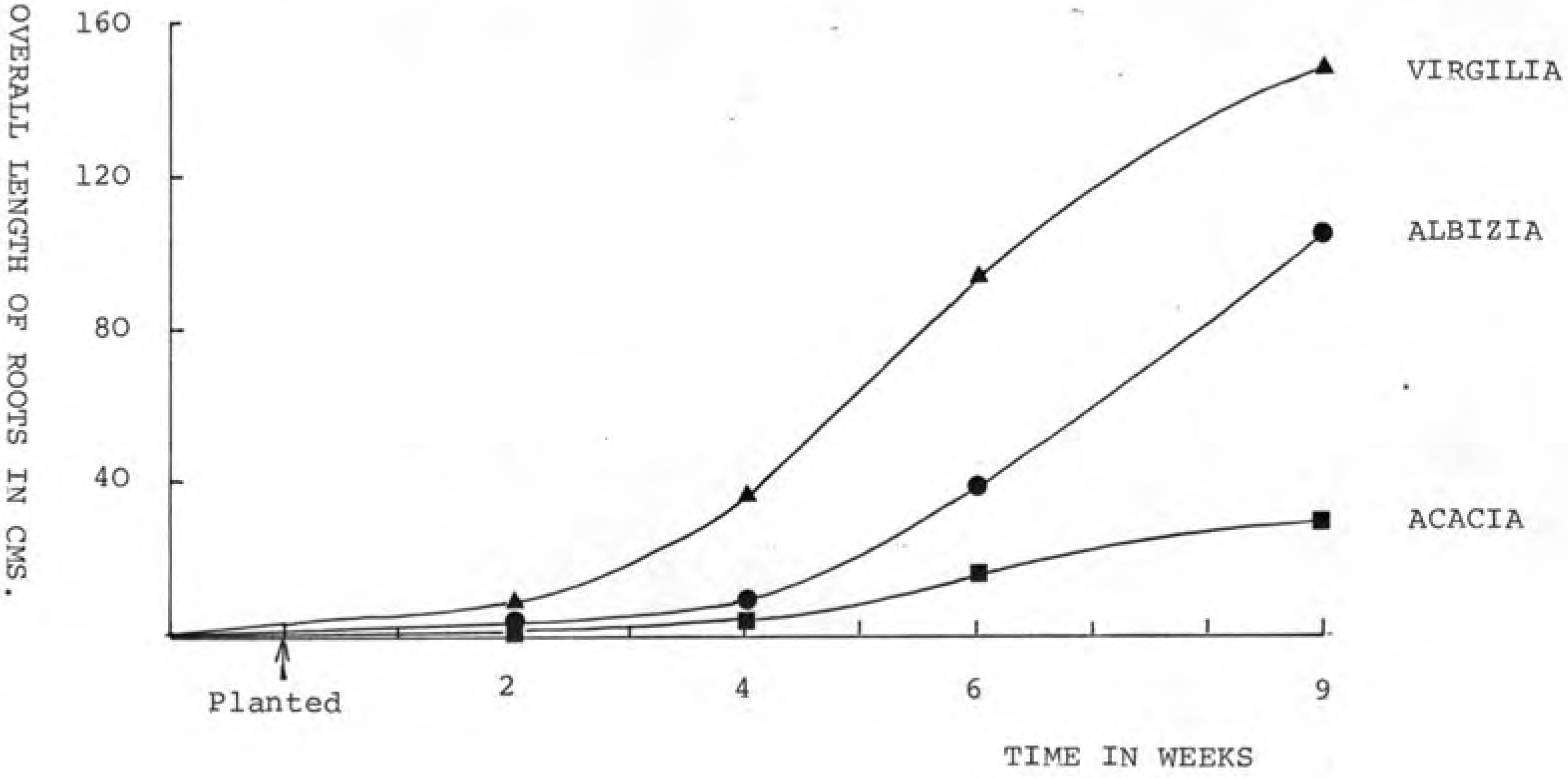
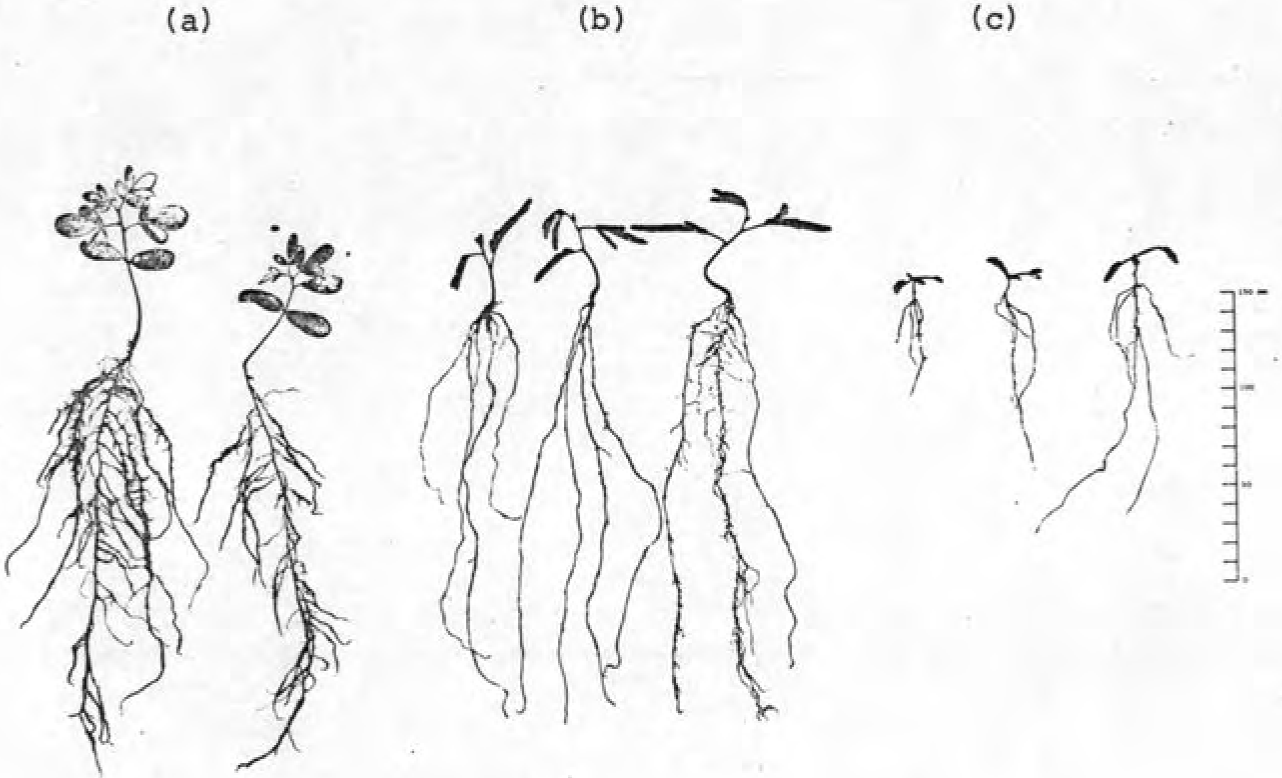


FIGURE 6C

SEEDLINGS GROWN FOR NINE WEEKS IN ROOT CHAMBERS WITH SOIL



(a) Virgilia
(b) Albizia
(c) Acacia

4.2. Root and shoot growth rates for each species when grown on pure vermiculite compared with that produced on vermiculite to which a nutrient is added.

4.2.1. Methods

The same experimental design and timing as described in Section 4.1.1. was used for measuring root and shoot growth rates in this experiment.

Instead of soil however, a Grade 3, coarse-grained vermiculite was used as a growth medium.

Three replicate seedlings for each species and for each treatment were grown in two sets of 9 root chambers.

To the first set of root chambers an application of 100 mls balanced nutrient solution was added to each seedling on a fortnightly basis for the full experimental 9 week growth period. Concentrations of the nutrients added were as follows:- $Ca(NO_3)_2 . 4 H_2O = 1.35$ g/l, $N_aNO_3 = 0,6737$ g/l, $Na H_2 PO_4 . 2H_2O = 0.4188$ g/l, $Na_2H PO_4 . 12H_2O = 0.4727$ g/l, $K_2 SO_4 = 0.7500$ g/l, $Mg SO_4 . 7H_2O = 0.5500$ g/l, $Ca Cl_2 . 2H_2O = 0.285$ g/l, FeNaEDTA = 0.0300 g/l, $H_3 BO_3 = 0.858 \times 10^{-3}$ g/l, $Mn Cl_2 . 4H_2O = 0.543 \times 10^{-3}$ g/l, $Zn SO_4 . 7H_2O = 0.066 \times 10^{-3}$ g/l, $Cu SO_4 . 5H_2O = 0.024 \times 10^{-3}$ g/l, $H_2 Mo O_4 . H_2O. = 0.006 \times 10^{-3}$

To the second seedling set no nutrients were added. However, it must be emphasized that ordinary tap water was used as a moisture source for all expetimental plants; hence non-nutrient treatment really represents 'very low nutrient' treatment.

All test vermiculite remained slightly acid/neutral at pH6-7 throughout the 9 week period.

The measurements were made in exactly the same manner as described in Section 4.1.

4.2.2. Analysis of data

Growth increments of shoots and roots were compared at each time interval for nutrient and non-nutrient treatments for each species separately. In addition, final dry weights for the seedlings were compared in the two treatments. Standard t tests were used to test significance throughout.

4.2.3. Results

With the exception of root growth in Albizia, there were no significant differences between rates, or overall shoot and root growths,of any of the test species grown with or without the added nutrient solution (Table 5A, Figures 7A, B,C). With Albizia, root growth was significantly reduced from week 6 to week 9 in the nutrient-treated plants, relative to the non-nutrient treated standards (Table 5A, Figure 7B).

Although the Albizia standards also showed a greater mean dry-weight value than the nutrient-treated plants, this was not found to be significant (Table 5B). (It may however imply a preference for very low nutrient levels.) Similarly, no significance was found between mean dry weights for the separate treatments in Virgilia and Acacia, both of which showed lower t - values than Albizia (Table 5B).

TABLE 5

PERFORMANCE WITH AND WITHOUT ADDED NUTRIENTS IN VERMICULITE

5A

COMPARATIVE RATES OF SHOOT AND ROOT GROWTH IN VERMICULITE, WITH AND WITHOUT ADDED NUTRIENTS FOR EACH SPECIES : t VALUES

$$t_{4}^{0.05} = 2.776$$

SPECIES		Number of Weeks			
		2	4	6	9
VIRGILIA	Shoots	0.543 (NS)	0.660 (NS)	0.369 (NS)	0.168 (NS)
	Roots	0.095 (NS)	.045 (NS)	0.028 (NS)	0.082 (NS)
ALBIZIA	Shoots	0.823 (NS)	0.420 (NS)	0.530 (NS)	1.810 (NS)
	Roots	2.180 (NS)	2.400 (NS)	3.37 (S)	3.56 (S)
ACACIA	Shoots	1.797 (NS)	0.94 (NS)	1.200 (NS)	0.580 (NS)
	Roots	0.503 (NS)	2.180 (NS)	1.48 (NS)	0.58 (NS)

5B

DRY WEIGHTS FOR EACH SPECIES WITH AND WITHOUT NUTRIENTS

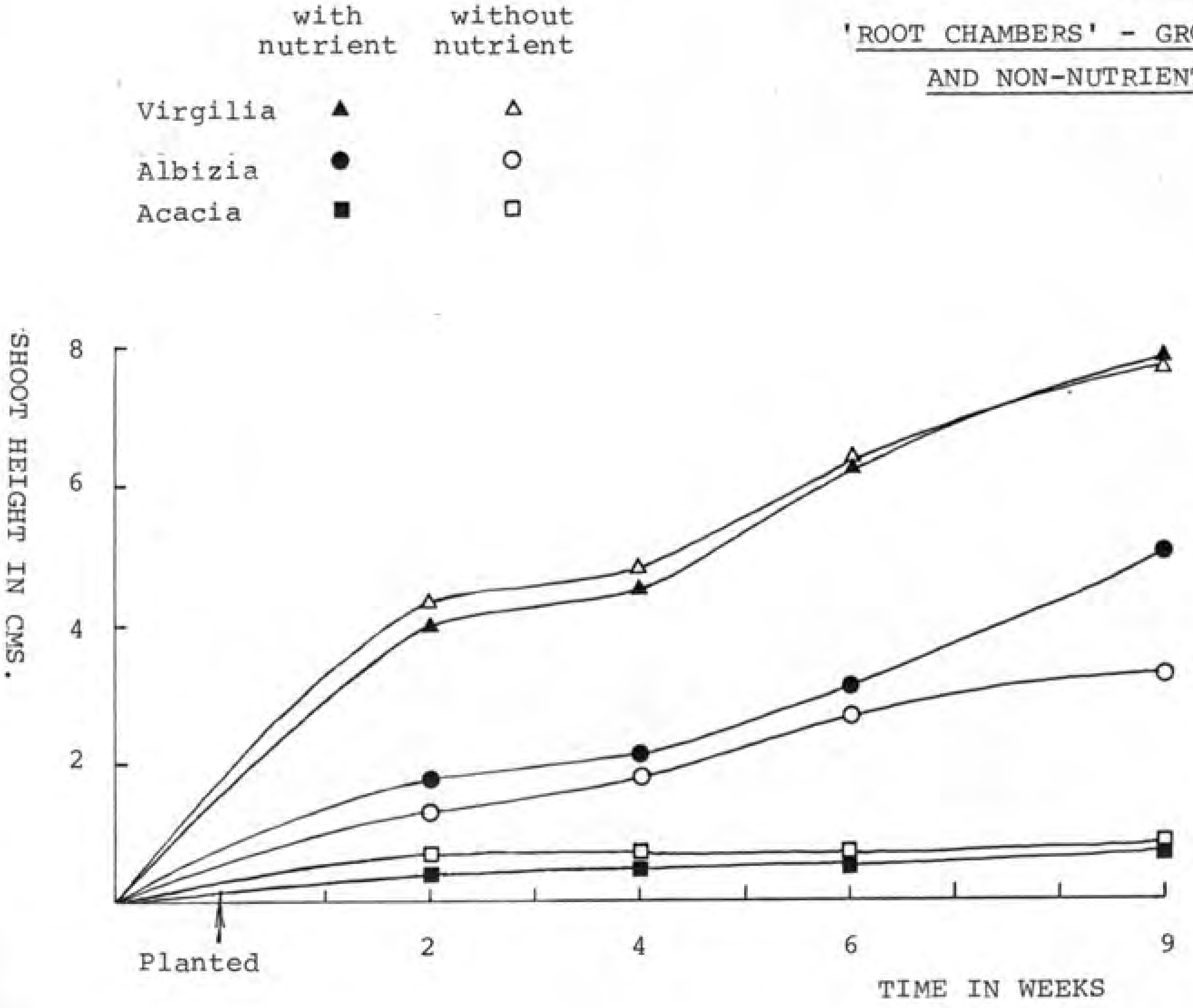
(t- VALUES COMPARE EFFECTS OF ADDED NUTRIENTS)

$$t_{4}^{0.05} = 2.776$$

SPECIES	TREATMENT	MEAN DRY WEIGHTS g	t - VALUES
VIRGILIA	With Nutrients	0.1952	0.395
	Without Nutrients	0.1841	
ALBIZIA	With Nutrients	0.1052	1.119
	Without Nutrients	0.1372	
ACACIA	With Nutrients	0.0176	0.626
	Without Nutrients	0.0145	

FIGURE 7A

'ROOT CHAMBERS' - GROWTH OF SHOOTS IN NUTRIENT AND NON-NUTRIENT TREATED VERMICULITE



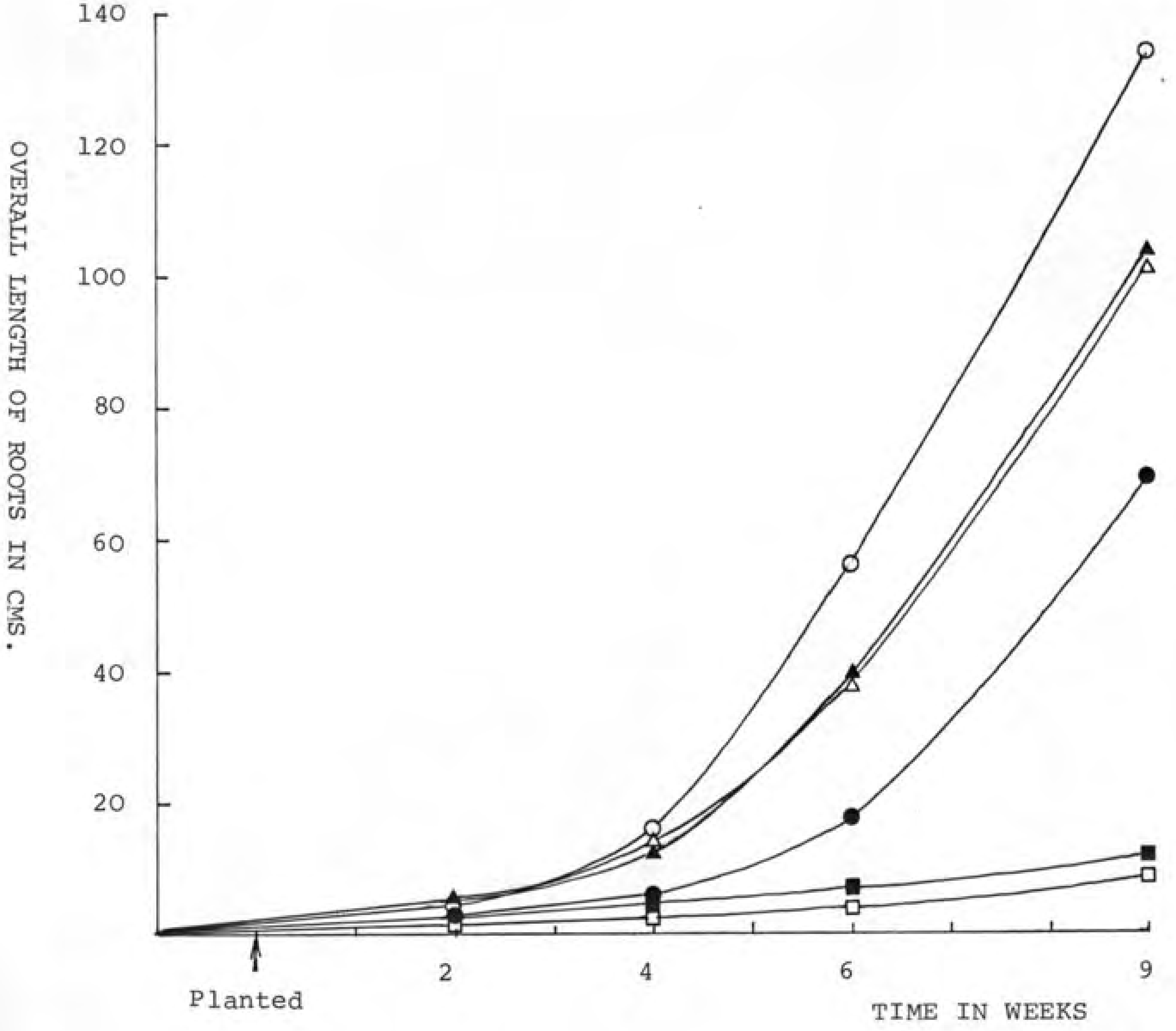


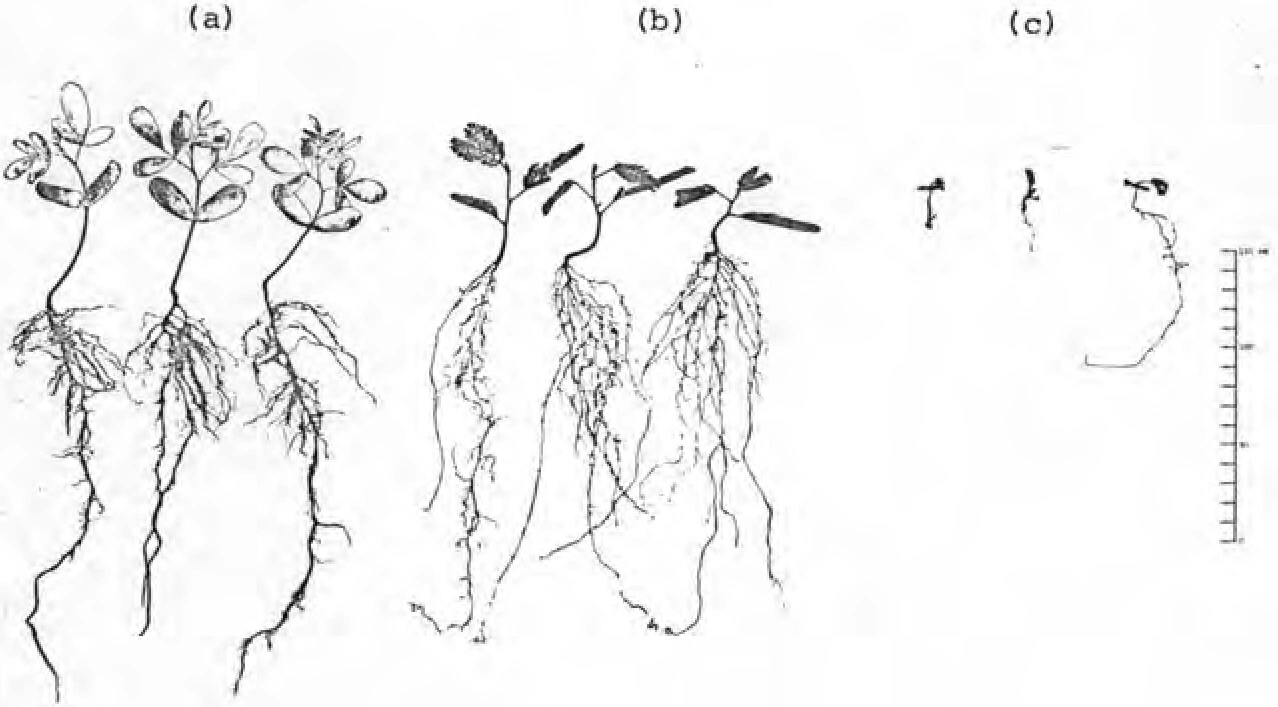
FIGURE 7B

'ROOT CHAMBERS'
GROWTH OF ROOTS IN
NUTRIENT AND NON-NUTRIENT
TREATED VERMICULITE

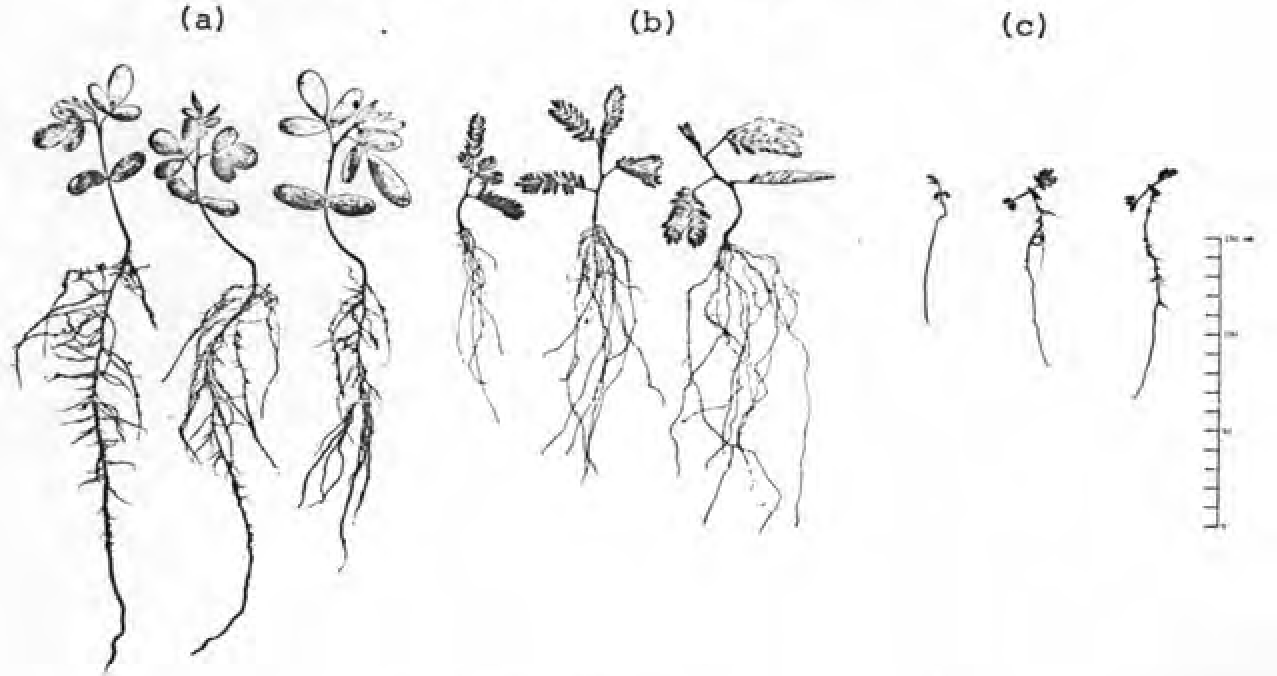
FIGURE 7C

SEEDLINGS GROWN FOR NINE WEEKS IN ROOT CHAMBERS WITH NUTRIENT AND NON-NUTRIENT TREATED VERMICULITE

(i) Nutrient treated vermiculite



(ii) Non-nutrient treated vermiculite



(a) Virgilia
(b) Albizia
(c) Acacia

TABLE 6

NUMBERS OF SEED PER POD, PERCENTAGES OF INFERTILE AND PREDATED SEED FOR RANDOM SAMPLES OF FIFTY SEED PODS TAKEN FROM SINGLE TREES FOR EACH SPECIES.

SPECIES	AVERAGE NUMBER OF SEEDS PER POD	PERCENTAGE OF INFERTILE SEED	PERCENTAGE OF SEED PREDATED
VIRGILIA	3.72	5.91	9.68
ALBIZIA	9.90	3.03	0.0
ACACIA	7.38	6.78	0.0

5. Some miscellaneous observations on natural seed and seedling predation as well as on overall seed productivity.

5.1. Methods

In order to estimate whether differential seed predation may be a factor in reducing regeneration rates of any one of the test species, small random samples of 50 seed pods were examined from individual trees of each species and the percentage of predated seeds was calculated. In addition, percentages of infertile seeds, as well as the average numbers of seeds per pod for each species, were measured.

Daily observations were also made on several seedlings of each species grown in the open during late autumn within a suburban garden, to establish which species appeared most susceptible to seedling predation.

5.2. Results

The average numbers of seed per pod and the percentages of seed found to be infertile are presented in Table 6. With single samples and fairly similar values between the species, it is difficult to draw definite conclusions from these two sets of data.

However, it does seem valid to conclude that predation is higher in the seed of Virgilia than in that of Albizia and Acacia; 9.68% predated in Virgilia may be compared with 0% in both Albizia and Acacia (Table 6). Moth larvae (undetermined species) are considered to be the chief Virgilia seed predators in the study sample.

The daily observation of seedlings grown out of doors unprotected from predators, revealed heavy nocturnal leaf-feeding activities by field crickets ([illegible]) on the Virgilia seedlings - in most cases leading to mortality within about a month after germination. In contrast, seedlings of

Albizia and Acacia remained unaffected by the crickets, and also apparently, by any other forms of visible predation . The same type of cricket has been observed during the late autumn in the field beneath Virgilia leaf litter (at Constantia Nek) and could therefore act as a truly natural agent of seedling control in Virgilia.

6. GENERAL DISCUSSION.

In connection with the seed germination tests it was found that the chipping of the micropylar ends of the seeds produced an extremely rapid germination in all the species. The results are comparable with those produced by the most effective seed germination enhancing treatments obtained by Clemens, Jones and Gilbert (1977), during germination tests on five Australian Acacias (including Acacia longifolia).

The various germination inhibitions recorded with increasing sensitivity in the order: Virgilia, Albizia, Acacia, are difficult to explain either on a technical or functional basis. Technically, some form of allelopathic interaction, similar to that described for Acacia cyclops and Acacia cyanophylla (now A. saligna) by Jones, Roux and Warren (1963) might operate in these cases. However, much recent criticism of earlier attempts to prove the presence of allelotoxins experimentally (Harper, 1977), precludes any direct conclusions about the exact nature of the inhibitions recorded. Oily exudates with strong aromatic odour, similar to that recorded for Casuarina littoralis litter in the inhibition of Eucalyptus ovata germination (Withers, 1977), were also noticed in the moistened macerated litters of all three test species. It is possible that some indirect inhibiting effect such as, for example, lowered oxygen availability produced as a result of litter decay, may have been operating, rather than an allelochemic reaction.

It does seem feasible that leaf litter and seedmix inhibitions, (whatever their exact cause), could probably operate in vivo. The existence of 'auto-inhibition', or mortality of germinating seeds due to decaying litter beds, beneath dense Acacia and Albizia stands, is supported by the observation that seed regeneration is absent in this case. However, it is more likely that this suggested type of inhibition is subsidiary to that of the enforced dormancy produced by impermeable seed coats; although the dormancy could become broken down by seed-coat decay etc. The tests also revealed that Acacia and Albizia seed are inhibited by the litters of one another as well as by that of Virgilia. This lack of specificity of action may well imply that many other types of litter could be inhibitory; trials with non-leguminous Kiggellaria africana litter appear to support this theory. Incidentally it is of interest to note that, among its other beneficial effects, such as the breaking of the primary enforced seed-coat dormancy, fire may act to remove any inhibitory organic material from around the seed-store (McPherson and Muller, 1969; Roux and Middlemiss, 1963). It is reasonable to suppose that interspecific seed-litter inhibitions could act in the field, and therefore artificially planted Virgilia may possibly, by means of its accompanying leaf litter, act to curb the regeneration of Acacia, Albizia seed stores.

The adequate disposal of the long-lived seed-stores of pest Australian legumes has proven the most intricate problem in their control; the coppicing of sawn-off trunk-bases of both species does not occur (pers. obs.). For instance, in combination with other control measures, the planting of Eragrostis curvula by the Grahamstown municipality in adjacent regions cleared of Acacia longifolia has so far successfully inhibited seed-store regeneration. Incidentally, Eragrostis seed was the only species found to be immune to inhibition by cold-water extracts of the closely-related Acacia cyclops and Acacia cyanophylla (saligna) (Jones et al, 1963).

Early seedling growth or vigour has often been correlated with seed weight or energy (Salisbury 1942, Grose and Zimmer, 1958) and thus may have some connection with the initial competitive vigour of the test species. However Albizia, although possessing the greatest seed energy, lagged behind Virgilia, both in overall shoot length, root length and biomass increments, as well as in competitive success. It could be argued that this results from the early shedding of the apparently non-photosynthetic cotyledons of Albizia, whereas the other two species retained their cotyledons as photosynthetic organs

throughout / -

throughout. However, *Albizia* appears to have quite sufficient energy to overtake *Acacia*, which possesses a far lower quantity, as well as quality, of seed energy than either *Albizia* or *Virgilia*.

Newman (1973) maintains that shoot competition for light is the one obvious factor which can produce a competitive advantage of one species over the other. Results from the 'replacement series' competition experiment tend to support this hypothesis: the increase of competitive inhibition for the three species corresponds with the increase in stem height. This correlation was also found in similar competition experiments involving seedlings of six Eucalypt species (Burdon and Pryor, 1975). Although this inference is valid, it cannot be fully verified unless the roots are isolated from one another during competition (Harper, 1977).

It is important to emphasize that, although the competitive enhancement/inhibition effects were largely significant at the stage of harvesting, the trends cannot be understood as necessarily representing the final outcome, because the percentage mortality was negligible (never exceeding 15 per cent for any of the species in any culture). Possible reasons why the present situation does not reflect the final outcome may involve certain characteristics of the autecologies of *Albizia* and *Acacia*. For example, both species can evidently produce greater lengths of root with less energy than *Virgilia*, permitting an increase of nutrient transfer into the shoots, which is vitally important for light competition. In *Albizia*, this is reflected by a later developing, slightly faster growth *rate* for both shoots and roots. With *Acacia*, the initial seed energy shortfall is slightly offset by the longer retention of photosynthetic seed cotyledons (up to 4 months, Milton, 1979), and also by the fact that no true phyllode leaves had developed during the course of the experiment. If the experiment was run for a longer period, it is possible that the more 'robust' true phyllodes may enhance the photosynthetic capacity of Acacia, thereby increasing the production of its relatively low-energy roots, and hence shifting the the competitive advantage into its favour. Research is continuing along these lines.

However, it could be speculated that if the application of water in the experiment had not been optimal, mortality in the mixed stands, relative to the pure, may have been higher in the competitively inhibited plants, as the effect of species dominance appears to be most significantly registered in the root biomass. If the latter were reduced in favour of an increase of energy to the shoots, in order to obtain access to the restricted light-"space", it is possible that the inhibited species may have become more susceptible to drought, in comparison with pure stand members; i.e. too great a rate of transpiration may occur, relative to the capacity of water-uptake.

Amongst other, in vivo, environmental factors which could alter the competitive balance between the species are differing moisture and nutrient availabilities of different soils (for example, Virgilia could represent a more vigorous competition when growing at optimal conditions in a rich clay-loam similar to the experimental soil), in which the moisture content ranges from 35 to 50 per cent (dry weight) (Phillips, 1926). However, Albizia may develop a competitive advantage over Virgilia in a poor leached soil, as evidenced by its slightly improved performance in the 'non-nutrient' vermiculite. An analogous situation may also apply in more advanced competition stages in which Albizia might tolerate lower nutrient levels. If this speculation is correct, would the addition of low fertilizer concentrations boost the competitive power of Virgilia over that of Albizia? Only further experimentation could answer this question.

If one concedes that Virgilia possesses a similar autecology to that of Albizia and Acacia, what is the prime reason for the latter's greater ubiquity (most obvious in the Cape Peninsula)? Present knowledge of the behaviour of invading species indicates that it is in the phases of germination and seedling establishment that their success or failure is most critically determined (Harper, 1969). The superficial in vivo examination of seed and seedling predation of the alien Albizia, Acacia relative to Virgilia reveals that at least part of the answer for Virgilia's comparative lack of establishment may lie in its greater susceptibility to predation. Phillips (1926) records several agents, in addition to those described, which are destructive to both regenerative and adult stages of Virgilia.

If ever some biological means for curbing the regeneration of Albizia and Acacia; similar to the insect control attempted for Hakea spp. (Neser, 1974, 1976), can be introduced, it seems reasonable to suggest that interspecific competition by Virgilia, might, if managed correctly, act as a subsidiary measure for the reclamation of Albizia and Acacia infested regions. Virgilia has the additional advantage in that it acts as a 'nurse stand' to permit the seral establishment of other indigenous trees (Phillips, 1926), which may also play a role in the further subjugation of Albizia and Acacia.

7. CONCLUSIONS

The observation of Harper (1969) that the most appropriate manner in which to detect differences in the ecologies of separate populations (or species) is to grow them together in mixture, has been,directly or indirectly,confirmed in this study. The broad hypothesis that the test legumes occupy similar ecological niches has definitely been verified, and in addition several important, although minor, autecological differences have been highlighted by the *comparative* approach which was adopted in the experimental procedure.

It has perhaps been demonstrated that the experimentation using samples sufficiently small, so as not to become counter-productive, can yield workable results. These results, analysed selectively, may have provided some insight into what is, broadly speaking, an attempt to channel research directly into solving a pressing and urgent problem - that of controlling or curbing pest-plant encroachment. Thus it is hoped that this article has opened an alternative avenue of approach to the subject of pest-plant control, i.e. the careful manipulation of our own biological resources.

Future research should also involve field trials, along the lines being followed at present by Professor Rycroft, who is planting experimental plots of *Virgilia* in *Acacia* infested mountain slopes at Banhoek Valley (C.P.). Also it may prove of value to investigate other indigenous species that could play a similar role to that proposed for *Virgilia* in 'out-competing' invasive woody plants.

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