Seedling vigour of some *Leucaena* spp. and their hybrids

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Abstract

The seedling vigour of 19 leucaena lines comprising principally the species *Leucaena leucocephala*, *L. pallida*, *L. diversifolia* and their hybrids was studied in glasshouse and field experiments in Hawaii between April and July 1991. Seedling vigour assessment was based on plant heights and plant weights during 84 days of growth. *L. pallida* and its hybrids with *L. leucocephala* gave more than twice the early growth of *L. leucocephala* cv. Cunningham or the common, weedy Hawaiian type, which were not significantly different. The early growth of the arboreal line, *L. leucocephala* K636, was greater than that of Cunningham, and its hybrids with *L. pallida* were outstanding. In the first 6 weeks of growth, *L. diversifolia* genotypes were less vigorous than *L. pallida* and, with the exception of CPI46568, were less vigorous than Cunningham. Days to emergence and growth at 16 days in the glasshouse were good indicators of subsequent growth potential both in the glasshouse and in the field. The implications of the results for breeding psyllid-resistant leucaena are discussed.

Introduction

Leucaena leucocephala is known for its slow seedling growth, which is often the major reason for failure of leucaena plantings in Australia (Lesleighter and Shelton 1986) and elsewhere. Slow growing seedlings are vulnerable to competition from vigorous weeds (Joenje and Kropff 1987) and predation by wildlife, and leucaena plants may take 3 years to reach a height of 2–3 m, when grazing can begin. This is discouraging to farmers wishing to use this highly productive species for animal production.

Another major barrier to increased leucaena production is the leucaena psyllid (*Heteropsylla cubana*). To combat this pest, it is imperative that psyllid resistance be incorporated into new leucaena selections. Similarly, cool tolerance to broaden the zones of climatic adaptation is desirable. Two species which are a source of genes to provide these characteristics are *L. pallida* and *L. diversifolia* (Wheeler and Brewbaker 1990). Both species have been hybridised with *L. leucocephala* in Hawaii (Sorensson and Brewbaker 1986) and progeny are being selected for cool tolerance and psyllid resistance. Psyllid resistance also exists in the species *L. esculenta* and *L. collinsii*, but little is known about their early vigour or agronomic potential.

Two experiments were conducted in Hawaii in 1991 to study the seedling vigour of 19 *Leucaena* lines. The experiments included psyllid-resistant and cool-tolerant species, their hybrids with *L. leucocephala* and arboreal lines of *L. leucocephala*. It is not known if arboreal types have better seedling vigour than shrubby types. These experiments will provide information on the agronomic characteristics of soon-to-be released psyllid-resistant and cool-tolerant hybrids from the University of Hawaii breeding programs.

Materials and methods

Glasshouse experiment

A glassshouse experiment was conducted at the University of Hawaii at Manoa from April 9 to July 2, 1991. Treatments were the 19 leucaena lines (Table 1), with 2 destructive yield harvests.

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Table 1. Leucaena lines planted in glasshouse and field experiments.

Species	Number/cultivar	Ploidy level	Source	Population
L. leucocephala	K636	4n	Waimanalo	OP[1] half-sib.
L. leucocephala	Cunningham (K500)	4n	Waimanalo	OP trees
L. leucocephala	Common (K997)	4n	Waimanalo	OP trees
L. pallida hybrid sib.	K806 × K748	4n	Waimanalo	hand sib.-cross
L. pallida	K804	4n	Waimanalo	OP trees
L. pallida	K376	4n	Waimanalo	OP trees
L. pallida	K819	4n	Waimanalo	OP trees
L. pallida	K953	4n	Waimanalo	OP trees
L. diversifolia	K156	4n	Waimanalo	OP half-sib.
L. diversifolia	K146	4n	Waimanalo	OP trees
L. diversifolia	CPI 46568	2n	Mealani	OP trees
L. collinsii hybrid sib.	K450	2n	Waimanalo	hand sib.-cross
L. diversifolia × *L. leucocephala*	K156 × K636	4n	Waimanalo	hand-cross
L. pallida × *L. diversifolia*	K806 × K156	4n	Waimanalo	hand-cross
L. pallida × *L. leucocephala*	K806 × K636	4n	Waimanalo	hand-cross
L. pallida × *L. leucocephala*	K748 × K636	4n	Waimanalo	hand-cross
(*L. diversifolia* × L. pallida) × *L. leucocephala*	(K784 × K376) × K636	4n	Waimanalo	hand-cross
L. esculenta	K948	2n	Mexico (OFI)	OP trees
L. lanceolata	K393	2n	Waimanalo	hand sib.-cross

[1]Open pollinated.

For the first harvest (4-week-old seedlings), a completely randomised design with 8 replications was used. For the second harvest (12-week-old seedlings), a randomised complete block design with 4 replications was used.

Pots were 9.5 and 22 cm in diameter for the first and second harvests, respectively, and contained 113 and 1150 g of air-dry soil medium, respectively. The medium was selected for ease of root washing and consisted of a mixture of peat moss (61%), perlite (22%) and vermiculite (17%). The medium was fertilised initially with 500 kg/ha of dolomite and Gaviota fertiliser which supplied the equivalent (in kg/ha) of 100 N, 46 P, 50 K, 0.2 Mg, 0.1 Mn, 0.5 Fe, 0.1 Cu, and 0.1 Zn. A solution of Gaviota was reapplied to seedlings for the second harvest after 3.5 and 8 weeks. The latter application caused some "leaf burn", from which plants subsequently recovered. To ensure sufficient micronutrients, a dilute solution of Gaviota was also applied weekly as a foliar spray from week 3.5. Plants were sprayed with Sevin (50% 1-napthyl-N-methylcarbamate by weight) at 1.5 ml/L, fortnightly after week 4, to control psyllids.

Insect-free seed of each line was obtained from the storage facility of the University of Hawaii Waimanalo Station on Oahu. Four lots of 50 seeds of each line were randomly selected for determination of mean seed weight. The seeds were then scarified in concentrated sulphuric acid for 7 minutes, rinsed, and soaked overnight in water. Only seeds which had imbibed water were planted. Three and 5 seeds were planted at 1 cm depth in the small and large pots, respectively, on April 9, 1991. Emergence was defined as the appearance of the cotyledons. Within 7 days of emergence, seedlings were thinned to 1 and 3 plants/pot for small and large pots, respectively, by discarding smallest and largest plants leaving plants of intermediate height. Plants were watered twice daily for 10 minutes by an automatic sprinkler system which maintained the potting medium near field capacity.

Mean plant height per pot was measured fortnightly. The 2 destructive harvests were made on May 21 (small pots) and July 2, 1991 (large pots), 4 and 12 weeks, respectively, after planting. Shoots, leaves and roots were separated, placed in paper sacks, and their dry matter determined following drying at 60°C for 48 hours in a forced-air oven. Leaf percentage was reported as a proportion of top growth, and root percentage as a proportion of total plant weight. Internode lengths were measured on seedlings in the large pots immediately prior to the 84-day harvest by halving the distance between ninth and eleventh internodes. Cotyledon area was calculated, assuming each cotyledon was an ellipse, from measurements of cotyledon length and width.

Field experiment

The field experiment was conducted at the Waimanalo Research Station (157° W, 21° N) of the University of Hawaii from April 11 to July 23, 1991. The same 19 lines were arranged in randomised complete blocks with 4 replications. Plots were single 4 m rows of each line with 1 m between rows and 20 cm between trees, giving 20 trees per plot. The soil was a fertile Isohyperthermic Vertic Haplustoll with a base saturation of 80%, no exchangeable Al and 15.5 meq/100g Ca. It receives an annual rainfall of 1100 mm. The field was cultivated to a fine seedbed just prior to planting. No fertiliser was applied.

Seeds were scarified and soaked as for the glasshouse experiment and planted singly into 5 cm-wide, peat, "Jiffy" pots filled with a mixture of peat and perlite on April 11, 1991. Pots were then sprayed with Captan fungicide and inoculated one week later with *Rhizobium* strain TAL 1145 obtained from NIFTAL (Paia, Maui). Seedlings were transplanted to the field on May 2. Weeds were controlled by hand-weeding and by applications of glyphosate as necessary. Plots were sprinkler irrigated 3 times per week initially, and then twice per week after June 11. As in the pot trial, plants were sprayed to control psyllids at recommended rates with Sevin at about fortnightly intervals. Plant heights were measured 42 and 84 days after transplanting.

Results

Waimanalo weather

Average monthly minimum and maximum temperatures ranged from 21.6 and 26.4°C in April to 23.5 and 28.9°C in July 1991, respectively. Monthly rainfall totals for this period were 63.8, 24.9, 23.1 and 8.9 mm, respectively. Average monthly relative humidity varied from 70–72%. Average monthly solar radiation varied from 20–23.8 MJ/m^2.

Seed weight and cotyledon area

There was substantial variation in mean seed weights, from a maximum of 117 mg/seed for *L. esculenta* to only 18 mg/seed for *L. diversifolia* CPI 46568 (Table 2). *L. pallida, L. leucocephala* and their hybrids had intermediate seed weights ranging from 33–66 mg/seed. *L. diversifolia* and *L. collinsii* lines were small-seeded (18–31 mg/seed) (Table 2).

Cotyledon area ranged from 1.15–6.98 cm^2 and was highly correlated with seed weight (R^2 = 0.89) (Table 3). Cotyledon area of *L. esculenta* was more than twice that of any other line.

Days to emergence

Mean number of days to emergence ranged from 4.0–9.5 days (Table 2). All *L. pallida* lines (except K376) and their hybrids were quick to emerge, with *L. diversifolia, L. leucocephala* and *L. collinsii* slow to emerge. An exception was *L. diversifolia* CPI 46568 which was intermediate (6.5 d). Days to emergence was significantly correlated with all other parameters except seed weight (Table 3). R^2 values for the correlations of days to emergence with height and weight at 84 days for the glasshouse experiment were 0.52–0.58 and 0.34 for height in the field. Germination rates were high for all seeds (90–100%) except for *L. collinsii* K450 sib. (70%).

Plant height

Seedlings could be divided into 4 groups on the basis of height at given ages using the mixture method of clustering applied to a 2-way data set reported by Basford and McLachlan (1985) (Figure 1). *L. pallida* and its hybrids with *L. leucocephala* K636 showed the most rapid height increase (group 1), with most lines exceeding 100 cm in the glasshouse and 160 cm in the field in 84 days (Table 2). Exceptions were the *L. pallida* lines, K376 and K819, which were intermediate in height (group 2). *Leucaena esculenta* showed rapid early growth but did not maintain this advantage. *L. lanceolata* was also intermediate in height.

L. diversifolia, L. leucocephala and *L. collinsii* were the least vigorous lines (group 4), achieving a height of only 40–75 cm in the glasshouse and 58–113 cm in the field over the same time period. *L. leucocephala* K636 (group 3) was superior to the other *L. leucocephala* lines in the glasshouse experiment. The hybrids of *L. diversifolia* and *L. pallida* with *L. leucocephala* K636 grew more rapidly than any of their parental lines.

Table 2. Growth characteristics of 19 leucaena lines in glasshouse (means/pot) and field experiments (means/plant).

Line	Seed wt	Glasshouse data								Field data	
		Cotyledon area	Days to emerg.	Ht 16d	Ht 84d	Plant wt[1] 84d	Leaf[2] 84d	Root[3] 84d	I'node length	Ht 84d	CV 84d
	(mg)	(cm^2)		(cm)	(cm)	(g)	(%)	(%)	(cm)	(cm)	(%)
L. leucocephala K636	66	2.65	8.5	3.5	75	18.5	57	39	5.7	91	14.0
L. leucocephala K500 (cv. Cunningham)	48	2.18	8.5	2.9	56	13.6	56	37	5.0	76	21.4
L. leucocephala K997 (common)	33	1.93	9.0	2.7	46	9.2	66	35	4.0	56	10.0
L. pallida K806 × K748	51	2.83	4.5	7.5	110	40.2	44	25	6.8	163	13.0
L. pallida K804	47	2.70	5.0	6.4	105	27.9	42	27	9.0	204	17.6
L. pallida K376	46	2.39	8.5	3.5	86	26.2	49	28	6.2	124	22.6
L. pallida K819	41	2.35	4.0	4.5	81	24.9	49	22	6.0	136	14.9
L. pallida K953	58	3.02	4.0	5.5	119	33.3	41	26	8.5	172	19.7
L. diversifolia K156	21	1.37	9.5	1.4	55	8.1	60	26	5.9	113	21.6
L. diversifolia K146	20	1.33	9.5	1.4	41	8.4	66	27	6.0	69	35.7
L. diversifolia CPI 46568	18	1.58	6.5	3.0	54	13.6	64	26	4.7	104	26.3
L. div K156 × L. leuc K636	23	1.67	8.5	2.8	89	24.9	51	34	7.6	174	44.3
L. pall K806 × L. div K156	37	2.24	4.5	4.8	82	26.5	47	25	7.4	76	13.6
L. pall K806 × L. leuc K636	39	2.31	4.3	4.7	100	37.5	46	30	7.9	197	17.2
L. pall K748 × L. leuc K636	45	3.40	5.0	6.1	126	38.0	43	30	9.6	214	9.0
[L. div K784 × L. pall K376] × K636	30	2.24	7.5	3.9	79	17.6	53	32	5.8	125	18.6
L. collinsii K450	22	1.15	8.5	2.0	40	5.0	74	31	4.4	58	39.9
L. esculenta K948	117	6.98	5.8	6.7	67	21.9	59	23	5.2	130	11.9
L. lanceolata K393	51	3.19	5.3	4.6	81	16.5	61	26	5.7	96	17.0
LSD $P<0.05$	6.0	0.48	0.9	0.9	20.5	8.7	7.2	5.5	1.7	35.8	
$P<0.01$	8.0	0.64	1.9	1.2	27.4	11.6	9.6	7.3	2.2	47.7	

[1]Whole plant weight.
[2]% of top growth.
[3]% of total weight.

Table 3. Coefficients of determination (R^2) ($P<0.05$) between growth parameters measured for 19 leucaena lines in glasshouse and field experiments.

Parameter	Seed wt	Glasshouse data												Field data	
		Cot. area	Days to emerg.	Ht 16d	Ht 42d	Ht 84d	Wt 42d	Wt 84d	Leaf % 42d	Leaf % 84d	Root % 42d	Root % 84d	I'node length	Ht 42d	Ht 84d
(a) Glasshouse data															
Seed wt															
Cot. area	0.89														
Days to emerg.	NS[1]	NS													
Ht 14d	0.41	0.49	0.67												
Ht 42d	NS	NS	0.61	0.74											
Ht 84d	NS	NS	0.52	0.60	0.77										
Wt 42d	0.44	0.43	0.51	0.81	0.82	0.59									
Wt 84d	NS	NS	0.58	0.64	0.76	0.87	0.65								
Leaf % 42d	NS	NS	0.56	0.65	0.82	0.75	0.73	0.86							
Leaf % 84d	NS	NS	0.45	0.49	0.76	0.85	0.55	0.82	0.83						
Root % 42d	0.21	NS	0.35	0.31	0.31	NS	0.29	NS	NS	NS					
Root % 84d	NS	NS	0.32	NS	NS	NS	NS	NS	NS	NS	0.34				
I'node length	NS	NS	0.32	0.30	0.59	0.76	0.34	0.62	0.52	0.71	NS	NS			
(b) Field data															
Ht 42d	NS	NS	0.48	0.69	0.89	0.74	0.75	0.74	0.71	0.75	NS	NS	0.64		
Ht 84d	NS	NS	0.34	0.41	0.58	0.74	0.47	0.68	0.54	0.64	NS	NS	0.70	0.77	

[1]Not significant.

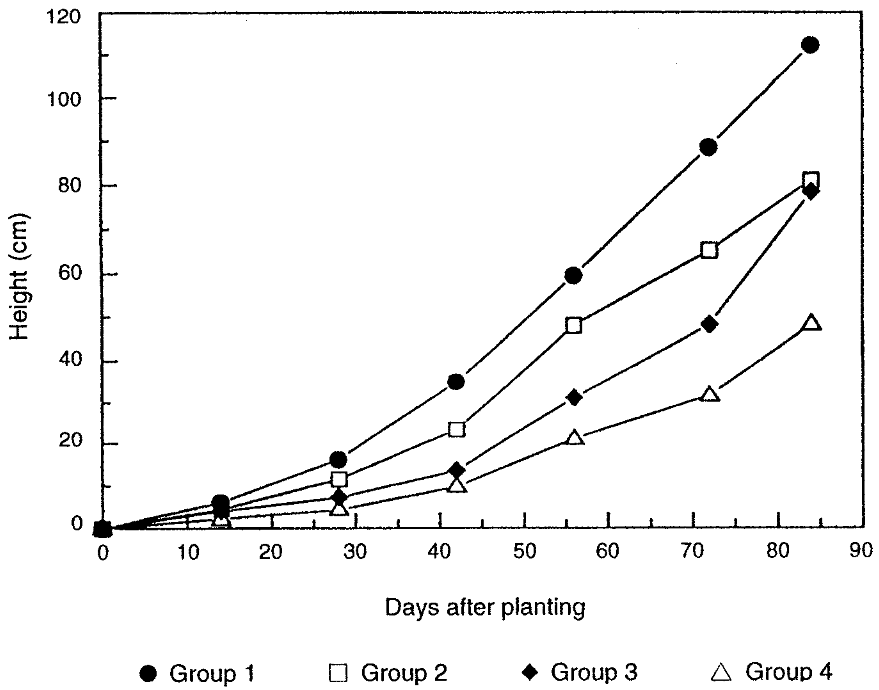

Figure 1. Height increments of leucaena lines showing high (Group 1), medium (Groups 2 and 3) and low (Group 4) vigour groups. Lines in each group are: Group 1 — K806 × K748, K804, K953, K806 × K636, K748 × K636; Group 2 — K393, K376, K819, K156 × K636, K806 × K156; Group 3 — K948, K636, (K784 × K376) × K636; Group 4 — Cunningham, K997, K156, K146, CPI 46568, K450.

Height increments in the field experiment closely followed patterns observed in the glasshouse. Correlation coefficients between glasshouse and field data obtained at 42 and 84 days were 0.89 and 0.74, respectively. There was also a significant correlation between the heights of 16-day-old plants in the glasshouse and those of 84-day-old plants, both in the glasshouse (R^2 = 0.60) and in the field (R^2 = 0.41) (Table 3).

Coefficients of variation for individual plant heights measured in the field experiment gave an indication of variability among the species. Data are not tabulated. The hybrid, *L. pallida* K748 × *L. leucocephala* K 636, and common leucaena were the least variable lines, with CVs of 9–10% after 84 days. In contrast, *L. diversifolia* lines and *L. collinsii* had CVs greater than 44 and 22% at 42 and 84 days, respectively. Both *L. pallida* K376 and *L. leucocephala* cv. Cunningham had high CVs relative to other lines of their species.

Plant weights

Plant weights mirrored plant heights in the glasshouse experiment (R^2 = 0.87 at 84 days) (Table 3). *Leucaena pallida* lines and their hybrids, except K819, produced most dry matter. The best *L. pallida* line (K806 × K748) and the 2 *L. pallida* hybrids with K636 produced more than twice the biomass of K636 and almost 3 times that of Cunningham. *L. diversifolia* lines and *L. collinsii* had the lowest weights but they were not significantly different from Cunningham and common leucaena.

Leaf and root proportions

The proportion of leaves in plant tops at 84 days in the glasshouse experiment ranged from 41–74% (Table 2). *L. pallida* and its hybrids had the lowest leaf percentage (41–49%), while *L. collinsii, L. lanceolata, L. diversifolia* and common leucaena K997 had the highest leaf percentages (56–74%). Other lines were intermediate. Leaf percentages at 42 and 84 days in the glasshouse experiment were closely related (R^2 = 0.83) (Table 3).

Root weight expressed as a percentage of whole plant weight ranged from 22–39% at 84 days (Table 2). Lines with low root percentages (22–28%) included *L. pallida, L. diversifolia, L. esculenta* and *L. lanceolata.* All *L. leucocephala* lines had high root percentages (35–39%). Other lines were intermediate.

Root percentage was not correlated with vigour indicators such as plant height or weight (Table 3).

Internode length

The range of internode lengths at 84 days was 4.0–9.6 cm (Table 2). *L. pallida* and its hybrids with *L. leucocephala* K636 had long internodes while *L. leucocephala, L. collinsii, L. esculenta, L. lanceolata* and diploid *L. diversifolia* had short internodes. Internode length at 84 days was well correlated with both plant height ($R^2 = 0.76$) and plant weight ($R^2 = 0.62$) (Table 3).

Discussion

Seedling vigour

Seedling vigour was equated with increases in plant height and weight. Ability to overtop weeds is a key to competitive success. Using these criteria, *L. pallida* and its hybrids with *L. leucocephala* produced the most vigorous seedlings in these experiments. In both glasshouse and field experiments, the best lines within this group grew 76–135% taller and had 105–196% greater shoot weights after 84 days of growth than Cunningham, the standard cultivar of *L. leucocephala* used in Australia. Therefore, programs to breed psyllid-resistant leucaena varieties by incorporating *L. pallida* genes are likely to improve seedling vigour. The poorer growth of *L. pallida* K376, relative to other *L. pallida* lines, was disappointing as K376 has been the major *L. pallida* parent in the breeding program at the University of Hawaii. Even so, height and weight of this genotype were still 54 and 93% greater, respectively, than Cunningham at 84 days of growth.

There was some evidence to support the hypothesis that arboreal *L. leucocephala* lines have better vigour than shrubby types. K636, an arboreal line, grew more rapidly than Cunningham in the glasshouse experiment, but was less vigorous than the *L. pallida* group. A similar result was obtained by Bray *et al.* (1988) when comparing seedlings of K8 with Cunningham and Peru. A surprising result in our experiment was the poor performance of Cunningham, which was not significantly better than common leucaena which is naturalised in the Hawaiian Islands. This latter variety is normally considered unproductive.

L. diversifolia lines were less vigorous than *L. pallida* and similar to Cunningham in the glasshouse experiment. In the field, K156 and CPI46568, tetraploid and diploid lines respectively, were similar and marginally taller than Cunningham. However, growth of *L. diversifolia* was poor for the first 6 weeks. The tetraploid line K146 had especially poor growth during early stages as did *L. collinsii.* Therefore, breeding programs which aim to combine the psyllid resistance or cool tolerance of *L. diversifolia* with the high quality of *L. leucocephala* will not increase seedling vigour to the same extent as hybrids with *L. pallida*. Growth of *L. lanceolata* was similar to that of *L. leucocephala* K636.

L. pallida hybrids showed strong evidence of heterosis for height but not for total plant weight and shoot weight. For this reason, the hybrid of *L. pallida* K376 × *L. leucocephala* K8 (parents of the KX2 hybrids in the University of Hawaii breeding program) can be expected to have good seedling vigour, even though the K376 parent was less vigorous than other *L. pallida* genotypes. Hybrid vigour may be reduced in successive generations due to inbreeding. There was also some segregation in the *L. diversifolia* × *L. pallida* hybrid for stunted seedlings, a characteristic not observed in other hybrids.

Indicators of seedling vigour

Several attributes measured early in the experiments were examined as possible early indicators of subsequent vigour. Although seed weight and cotyledon area more highly correlated with growth during the first 16 days, their influence declined as the experiment progressed. This result is in accord with findings of other workers that seed weight is correlated with early but not with later stages of seedling growth (Black 1959; Hendrix *et al.* 1991).

Days to emergence was a surprisingly good indicator of subsequent vigour. This parameter explained 52 and 58% of the variation in plant height and plant weight, respectively, at 84 days in the glasshouse experiment, although the equivalent value for the field experiment was only 34%. Time to emergence was also significantly correlated with root % (R^2 = 0.32 and 0.35) and was the only parameter to maintain a relationship with the proportion of plant growth partitioned to roots through to the end of the experiment. Seeds were carefully scarified, ruling out hardseededness as the basis for differences in days to emergence. Time to emergence was not correlated with seed weight.

The best indicator of subsequent plant height and weight was height at 16 days, which was significantly correlated with subsequent growth data from both glasshouse and field experiments. Early plant height may be a useful early indicator of subsequent seedling vigour. There was also good evidence that glasshouse data collected from plants growing in an artificial medium regularly fertilised with a complete and balanced nutrient solution correlated well with field results. These results indicate that rapid screening of large numbers of accessions for seedling vigour is feasible under controlled conditions with the opportunity for substantial savings in costs and resources.

Leaf and root percentage

Leaf percentage varied from 41–74% at the end of the experiment and was highly and negatively correlated with both plant height and weight (R^2 = 0.49–0.85). The tallest plants, i.e. *L. pallida* lines and their hybrids with K636, had the lowest leaf percentages. It is not known if this result is due to genotypic characteristics or to allometric reductions in leaf percentage as plants increase in size. In the present study, the tallest plants had the longest internode lengths (Table 2). If this trend continued to maturity, leafiness may be lower in *L. pallida* and its hybrids (Figure 2). The internode lengths of mature *L. pallida* trees were typically 2–5 times greater than those on *L. leucocephala* and *L. diversifolia* trees. Leafiness of arboreal *L. leucocephala* genotypes such as K636 was slightly lower than that of shrubby types such as Cunningham.

Root percentage was not correlated with growth indicators at 84 days and appeared to be a parameter characteristic of the particular

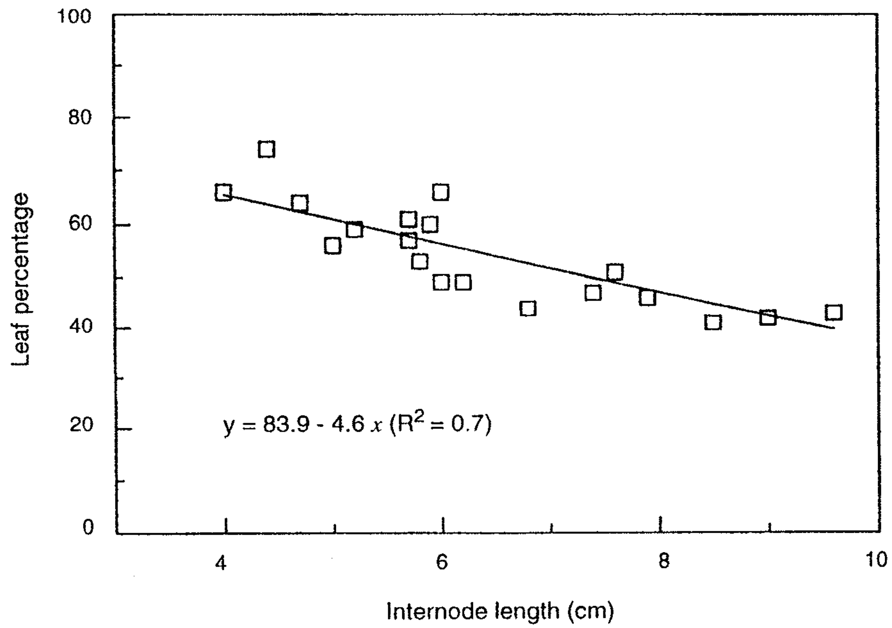

Figure 2. Relationship of leaf percentage with internode length for 19 leucaena lines after 84 days of growth.

species. For instance, *L. leucocephala* lines and their hybrids had higher root percentages than other lines, except for *L. collinsii*. This may partly explain the poorer seedling growth of this species relative to that of *L. pallida* as a greater proportion of the products of photosynthesis were partitioned to the roots. This characteristic, however, may result in improved growth in mature trees relative to *L. pallida* due to more effective root systems although this aspect was not studied in the present experiment.

Conclusions

These experiments indicate that *L. pallida* lines and their hybrids with *L. leucocephala* have substantially better seedling vigour than either *L. leucocephala* or *L. diversifolia* lines. Hybridisation between *L. leucocephala* and *L. pallida* may therefore improve both seedling vigour and psyllid resistance of the former species. Unfortunately, little is known of the forage quality of *L. pallida* and its hybrids and this aspect requires further study. The work of Austin *et al.* (1990) indicates moderate digestibility in *L. pallida* K376.

Results indicate that seedling height at 2 weeks is well correlated with height at 12 weeks. This offers the opportunity for rapid screening of large numbers of accessions for seedling vigour in a controlled glasshouse environment. Initial screening could be based on both days to emergence and seedling vigour, and possibly psyllid resistance, greatly reducing the number of lines that need to be field tested.

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(Received for publication October 16, 1992; accepted January 6, 1994)