GENETIC VARIATION IN A SECOND-GENERATION PROGENY TRIAL OF *ACACIA AURICULIFORMIS* IN THAILAND

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Received November 2000

LUANGVIRIYASAENG, V. & PINYOPUSARERK, K. 2002. Genetic variation in a second-generation progeny trial of *Acacia auriculiformis* in Thailand. Open-pollinated seed from selected families from a first-generation progeny trial/seedling seed orchard of *Acacia auriculiformis* was used to establish second-generation progeny trials. There were 106 families, of which 13 were descended maternally from three Thai land races (candidate plus trees), 47 from four Papua New Guinea provenances, 25 from six Queensland provenances and 21 from seven Northern Territory provenances. In addition, two unimproved families from a local Thai land race were included for comparison. Assessment was made at age 36 months for height, diameter at breast height and individual tree volume, and at age 40 months for stem form (axis persistence and stem straightness) and branching habit (presence of upright branches on the lower part of the stem, repeated forking on the multiple stems and branch thickness). All families from the first-generation seedling seed orchard grew significantly faster than local unimproved seed trees. Families maternally descended from the Queensland region were most productive, followed by those from Papua New Guinea, Northern Territory and Thailand. Despite a considerable increase in growth rate over unimproved seed trees, families descended from the Thai land races were clearly out-performed by those originating from Australia and Papua New Guinea. Most families produced single-stemmed trees with good stem axis persistence and a low frequency of upright branches on the lower part of the stem, indicating a considerable improvement in the stem form over the first generation. Estimates of individual-tree, narrow-sense heritabilities for most growth and form parameters were low, but statistically significant, ranging from 0.06 for repeated forking to 0.20 for stem straightness. Heritability was not significant for presence of upright branches.

Key words: *Acacia auriculiformis* - progeny trial - genetic variation - height - diameter - stem form - branching habit - heritability - Thailand

LUANGVIRIYASAENG, V. & PINYOPUSARERK, K. 2002. Variasi genetik dalam percubaan progeni generasi kedua *Acacia auriculiformis* di Thailand. Percubaan progeni generasi kedua telah ditubuhkan daripada biji benih pendebungaan bebas yang diperoleh daripada kajian progeni/kebun anak biji benih *Acacia auriculiformis* generasi pertama. Daripada 106 famili, 13 diwariskan secara maternal daripada tiga ras

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daratan Thai (calon pokok terbaik), 47 daripada empat provenans Papua New Guinea, 25 daripada enam provenans Queensland dan 21 daripada tujuh provenans Wilayah Utara. Di samping itu, dua famili yang tidak diperbaik daripada ras daratan tempatan di Thai dimasukkan untuk perbandingan. Penilaian dibuat untuk ketinggian, garis pusat aras dada dan isipadu pokok individu pada umur 36 bulan. Penilaian bentuk batang (ketahanan paksi dan kelurusan batang) dan tabiat pendahanan (kemunculan dahan-dahan tegak pada bahagian bawah batang, cabangan berulang di batang berbilang dan ketebalan dahan) pula dibuat pada umur 40 bulan. Kesemua famili daripada kebun anak biji benih generasi pertama tumbuh lebih cepat dengan bererti berbanding pokok biji benih tempatan yang tidak diperbaik. Famili yang diwariskan secara maternal daripada kawasan Queensland paling produktif, diikuti famili daripada Papua New Guinea, Wilayah Utara dan Thailand. Famili ras daratan Thai mengalami pertambahan kadar pertumbuhan yang ketara berbanding pokok biji benih yang tidak diperbaik. Walau bagaimanapun prestasinya jelas lebih rendah berbanding famili yang berasal daripada Australia dan Papua New Guinea. Kebanyakan famili menghasilkan pokok berbatang tunggal dengan ketahanan paksi batang yang baik dan frekuensi dahan tegak yang rendah di bahagian bawah batang. Ini menunjukkan bahawa terdapat pembaikan yang ketara dalam bentuk batang berbanding generasi pertama. Anggaran pokok individu, keterwarisan keertian sempit bagi kebanyakan parameter pertumbuhan dan bentuk adalah rendah tetapi bererti dari segi statistik, berjulat antara 0.06 bagi cabangan berulang hingga 0.20 bagi kelurusan batang. Keterwarisan adalah tidak bererti bagi kemunculan dahan tegak.

Introduction

Acacia auriculiformis is one of the most common exotic trees in Thailand and has become a part of the landscape with tens of thousands of hectares of plantations and millions of scattered trees planted around farms, homesteads, roads and villages. The species was first introduced from Australia in 1935 and has proved to be very adaptable to a wide range of soil and climatic conditions. It is fast growing, reaching 15 m tall in five years under favourable conditions (Pinyopusarerk 1990). It is an excellent shade tree and the wood has many uses, including firewood, furniture and construction. However, *A. auriculiformis* in Thailand has a tendency to produce multiple leaders and crooked stems, limiting its use as poles or other forms of timber that require reasonable length. Repeated forking often occurs on the multiple stems which further reduces the usability of each individual stem. Although single-stemmed trees can be found, they tend to retain one or more upright branches, especially on the lower part of the stem. These upright branches were competing leaders at the early stage of development and, although failing to become the main leader, they remain visible on the lower part of the main stem of mature trees. These characteristics are undesirable as far as utilisation and timber quality are concerned.

A tree improvement program for *A. auriculiformis* in Thailand was started in 1984 by the Royal Forest Department with the aim of improving the growth and stem form of the species. Candidate plus trees, based on vigour and straight clear bole > 6 m in length were selected from planted and naturalised stands throughout the country. Open-pollinated seed was collected from these candidate plus trees to form the first breeding population. In addition, seed from natural populations in

Australia and Papua New Guinea was supplied by the CSIRO Australian Tree Seed Centre. The first series of progeny trials were established on three sites in 1989. Reports on these trials indicated considerable variation in growth and stem form between families within provenances, between provenances with regions and between regions (Luangviriyasaeng *et al.* 1995). Of particular note was the much poorer growth of Thai candidate plus trees in comparison with new introductions from Australia and Papua New Guinea. These trials have been converted to seedling seed orchards (SSO) by selective thinning, with the best tree retained in each original five-tree plot, and some inferior families removed from the trials. In order to maintain a broad genetic base for breeding, only the worst performing families were removed from the first-generation SSO at Sakaerat, north-eastern Thailand, prior to seed collection for the second-generation trial described here. In 1993, open-pollinated seed was collected from the best individual tree of each retained family for testing in second-generation progeny trials planted in 1994. An earlier report on these second-generation trials by Pinyopusarerk *et al.* (1998) dealt only with the variation in the growth rates up to 24 months without regard to other economically important traits such as stem form and branching habit. In this report the variation in growth rates and qualitative characteristics, assessed at 36 and 40 months respectively is examined for one of the second-generation trials.

Materials and methods

Seedlots

A total of 106 seed trees from the first-generation SSO at Sakaerat was selected based on their better-than-average vigour and bole length for each of the respective provenance origins. These 106 trees included 13 trees descended maternally from three local land races (candidate plus trees from three different regions of Thailand), 47 trees descended from four original Papua New Guinea provenances, 25 trees descended from six Queensland provenances, and 21 trees descended from Northern Territory provenances. In addition, two seed trees from a local unimproved land race were included as control (Table 1). Seedlings from the 108 open-pollinated seed families were raised at a local nursery for about five months before out-planting in August 1994.

Site and layout

The planting site is located at a forest research station at Kuiburi, Prachuap Khiri Khan province (latitude 12° 05' N, longitude 99° 45' E, altitude 30 m). The mean annual rainfall is 1180 mm and the mean annual temperature is 27.4 °C. The soil is sandy loam, pH 7.3. Site preparation included disc-ploughing twice in cross directions. Within two months after planting 100 g of NPK fertiliser (15:15:15) was applied to each plant. Weed competition was kept to a minimum in the first two years by manual weeding.

The experimental design was a resolvable row-column design (Williams & Matheson 1994). The design generation package ALPHA + (Williams & Talbot 1993) was used to produce randomisations for eight replicates. To further increase the effectiveness in the randomisation the 108 families were grouped into five regions, namely, Thailand, Papua New Guinea,Queensland (Australia), Northern Territory (Australia) and local (unimproved). Each replicate contained 14 rows and 8 columns, in total 112 plots per replicate. Plots allocated to treatment numbers 109 to 112 were filled with seedlings from among the 106 seed orchard families, but not included in the data analysis. Each family plot consisted of a row of four trees spaced at 1.5 m between trees. The space between rows was 3 m.

Table 1 List of families of *Acacia auriculiformis* planted in a second-generation progeny trial in Thailand

Region	Seed source no.	Origin of mother trees	No. of parent trees
Thailand	1	Prachuap Khiri Khan	7
	2	Nakhon Ratchasima	1
	3	Rayong	5
		Subtotal	13
Papua New Guinea	4	Bensbach	3
	5	Balamuk	5
	6	Mibini	36
	7	Old Tonda Village	3
		Subtotal	47
Queensland Australia	8	SW of Coen River	3
	9	WNW of Coen River	5
	10	S of Coen	5
	11	Wenlock	8
	12	Morehead River	1
	13	Kings Plain	3
		Subtotal	25
Northern Territory Australia	14	Manton River	1
	15	Douglas River	5
	16	Goomadeer River	3
	17	Mann River	8
	18	Alligator River	1
	19	Elizabeth River	1
	20	Melville Island	1
		Subtotal	21
Local unimproved seed trees	21	Kuiburi	2
		Subtotal	2
		Total	108

Assessment

At 36 months after planting, all surviving trees were measured for height (H) and diameter at breast height (D). Individual conical tree volume (V) was then calculated using the expression

$$V = 1/3\pi(D/2)^2 H.$$

In addition, all trees, at 40 months of age, were scored subjectively for five morphological characteristics:

(1) axis persistence (reflected the ability of the tree to retain its primary axis): six classes
- (a) double or multiple leaders from ground level
- (b) axis lost persistence in the first (lowest) quarter of the tree
- (c) axis lost persistence in the second quarter of the tree
- (d) axis lost persistence in the third quarter of the tree
- (e) axis lost persistence in the fourth quarter of the tree
- (f) complete persistence

(2) stem straightness (recorded only for trees which scored 4–6 in the axis persistence): four classes
- (a) very crooked, 2 or more serious bends
- (b) slightly crooked, 1 serious bend and/or > 2 small bends
- (c) almost straight, 1–2 small bends
- (d) completely straight

(3) presence of upright branches in the first quarter of the stem from ground: four classes
- (a) multiple upright branches
- (b) single, diameter > 1/2 of main stem
- (c) single, diameter < 1/2 of main stem
- (d) none

(4) repeated forking on multiple stems: two classes
- (a) repeated forking
- (b) no repeated forking

(5) branch thickness (excluding the living, upright branches): four classes
- (a) very heavy, > 2 branches with diameter > 1/3 of the main stem
- (b) heavy, 2 branches with diameter > 1/3 of the main stem
- (c) light, 1 branch with diameter > 1/3 of the main stem
- (d) very light, branch diameter ≤ 1/3 of the main stem

Analysis

The software package DataPlus Version 2 was used to pre-process the data and to generate Genstat code for the statistical analysis by the Genstat 5 software package (Payne *et al.* 1987). Following Williams and Matheson (1994), plot means were analysed using a mixed model where replicates and families were treated as fixed effects and row and column within replicates were treated as random effects. Residual maximum likelihood (REML) procedure for mixed models was used to estimate the family mean of each trait. Estimated family means were then analysed using one-way analysis of variance to incorporate the treatment structure present in the families, namely regions and provenance origins within regions.

Genstat outputs indicated the experimental units that had unusually large residuals. These were treated as missing values in the data analysis.

Heritability (h^2)

Variance components were obtained by mixed model analyses which treated family, row and column within replicate as random effects and region of origin and replicate as fixed effects. The two local land race families were excluded from the data set for the heritability calculations. Region was specified as a fixed effect in the heritability calculation because observations at the Sakaerat SSO showed that the trees from Northern Territory provenances had a flowering peak some two months in advance of those from Papua New Guinea and Queensland, and were thus effectively reproductively isolated from them. Narrow-sense, individual-tree heritabilities (h^2) were estimated using the expression

$$h^2 = 1/r * \sigma_f^2/(s_f^2 + \sigma_m^2 + \sigma_t^2)$$

where σ_f^2, σ_m^2, and σ_t^2 are variance components for families, between plots and between trees within plots respectively. The coefficient of relationship (r) used in computation of individual tree heritabilities was taken as 0.33 (Williams and Matheson 1994).

Results

Survival was generally high (greater than 90%) for most families and therefore will not be discussed further.

Growth

Except for differences in diameter at breast height (dbh) between provenance origins within regions, there were significant differences in height, dbh and tree volume between regions, provenance origins within regions and families within provenance origins ($p < 0.05 - < 0.01$) (Table 2). Seedlot means for height, dbh and tree volume are shown in Table 3.

Table 2 Mean squares from analyses of variance for eight growth traits in a second-generation progeny trial of *Acacia auriculiformis* in Thailand

Source of variation	Degrees of freedom	Height	dbh	Tree volume	Axis persistence	Stem straightness	Upright branches	Repeated forking	Branch thickness
region	4	84.0657**	131.6233**	307509**	20.2380**	0.6007^{ns}	0.5414**	0.6220*	1.7178^{ns}
region.provenance	16	3.3852*	3.3782^{ns}	11466*	1.4262^{ns}	0.9623^{ns}	0.0375^{ns}	0.1551^{ns}	0.7153*
region. provenance.family	85	1.7103**	1.9376**	5436**	0.9730**	0.5617**	0.4619^{ns}	0.1409*	0.3364**
residual	$677^{\#}$	0.9877	0.8534	2315	0.5495	0.222	0.0483	0.1083	0.2173

* and ** indicate sifnificant difference at $p < 0.05$ and $p < 0.01$.
ns indicates no significant difference at $p < 0.05$.
# indicates actual residual degrees of freedom varied between traits as some outlying values were omitted.

Table 3 Seedlot means for growth at 36 months and stem form and branching habit at 40 months along with range of family means in a second-generation progeny trial of *Acacia auriculiformis* in Thailand

Seed source	Origin of mother trees	No. of families	Height (m)			Dbh(cm)			Tree volume ($\times 10^{-4}$ m^3)		
			Prov.	Fam.	Fam.	Prov.	Fam.	Fam.	Prov.	Fam.	Fam.
Thailand region	Prachuap Khiri Khan	7	9.4	8.3	10.2	6.4	5.6	7.2	121.1	92.2	150.8
	Nakhon Ratchasima	1	9.3	9.3	9.3	6.5	6.5	6.5	118.4	118.4	118.4
	Rayong	5	9.3	8.8	10.2	6.6	6.2	7.2	127.1	113.8	146.2
Mean			9.4			6.5			123.2		
Papua New Guinea region	Bensbach	3	10.3	9.6	10.7	8.5	7.9	9.0	217.3	180.4	244.2
	Balamuk	5	10.2	9.9	10.4	8.6	8.3	8.9	213.4	198.4	229.8
	Mibini	36	10.4	9.2	11.4	8.3	7.1	9.4	208.8	148.2	272.6
	Old Tonda Village	3	10.4	9.7	10.9	8.4	8.0	8.9	212.9	187.6	239.0
Mean			10.3			8.4			210.2		
Queensland region	SW of Coen River	3	10.9	10.5	11.1	8.3	8.1	8.5	217.0	207.7	222.8
	WNW of Coen River	5	10.8	10.3	11.4	8.5	7.9	9.0	226.9	197.7	258.1
	S of Coen	5	10.8	10.3	11.2	8.6	8.1	9.5	229.3	195.4	274.3
	Wenlock	8	10.9	10.3	11.1	8.6	7.4	9.7	229.9	162.6	281.8
	Morehead River	1	11.4	11.4	11.4	9.2	9.2	9.2	270.0	270.0	270.0
	Kings Plain	3	11.8	11.4	12.1	9.3	8.9	9.5	280.7	242.8	300.9
Mean			11.0			8.7			235.3		
Northern Territory region	Manton River	1	10.9	10.9	10.9	8.6	8.6	8.6	219.4	219.4	219.4
	Douglas River	5	10.5	10.1	10.9	7.8	7.4	8.5	179.6	160.0	205.0
	Goomadeer River	3	10.3	10.1	10.4	8.0	7.8	8.2	191.9	174.4	209.1
	Mann River	2	11.2	11.0	11.4	8.8	8.5	9.0	244.2	231.1	257.3
	Alligator River	8	10.1	9.3	10.5	7.7	6.7	8.2	179.8	134.3	204.6
	Elizabeth River	1	11.1	11.1	11.1	8.1	8.1	8.1	190.1	190.1	190.1
	Melville Island	1	9.2	9.2	9.2	6.5	6.5	6.5	116.3	116.3	116.3
Mean			10.4			7.9			187.0		
Local unimproved trees	Kuiburi	2	7.2	6.9	7.5	4.7	4.7	4.8	57.2	56.8	57.6
Trial mean			10.3			8.1			198.1		
SED region (ANOVA)			0.2			0.1			7.5		
SED provenance (ANOVA)			0.4			0.3			17.5		
SED family (REML)			0.5			0.5			24.3		
h^2			0.11			0.14			0.16		

continued

Table 3 (continued)

Seed source	Origin of mother trees	Axis persistence			Stem straightness			Upright branches			Repeated forking			Branch thickness		
		Prov.	Fam.	Fam.	Prov.	Fam.	Fam.	Prov.	Fam.	Fam.	Prov.	Fam.	Fam.	Prov.	Fam.	Fam.
Thailand region	Prachuap Khiri Khan	4.2	3.6	4.7	1.5	1.3	1.8	3.8	3.7	4.0	1.4	1.2	1.6	2.7	2.3	2.9
	Nakhon Ratchasima	4.1	4.1	4.1	1.3	1.3	1.3	3.8	3.8	3.8	1.3	1.3	1.3	2.4	2.4	2.4
	Rayong	4.0	3.8	4.1	1.6	1.2	1.2	3.8	3.7	3.8	1.5	1.4	1.6	2.6	2.3	3.0
Mean		4.1			1.5			3.8			1.4			2.6		
Papua New Guinea region	Bensbach	4.2	3.6	4.7	1.4	1.2	1.6	3.9	3.8	3.9	1.4	1.3	1.5	2.3	2.2	2.5
	Balamuk	4.1	3.6	4.5	1.7	1.5	1.8	3.8	3.7	3.9	1.4	1.2	1.5	2.6	2.5	2.7
	Mibini	4.5	3.5	5.1	1.7	1.3	2.2	3.9	3.8	4.0	1.5	1.1	1.8	2.7	2.3	3.1
	Old Tonda Village	4.2	3.8	4.8	1.5	1.5	1.6	3.9	3.8	4.0	1.5	1.4	1.6	2.5	2.3	2.8
Mean		4.4			1.7			3.9			1.5			2.6		
Queensland region	SW of Coen River	4.9	4.8	5.0	1.6	1.3	1.8	3.9	3.8	3.9	1.6	1.5	1.6	2.9	2.8	2.9
	WNW of Coen River	4.7	4.4	5.1	1.8	1.4	2.2	3.9	3.8	4.0	1.6	1.5	1.8	2.8	2.4	3.1
	S of Coen	4.6	4.2	5.0	1.6	1.4	1.9	3.9	3.6	4.0	1.5	1.3	1.6	2.5	2.4	2.8
	Wenlock	4.5	4.2	5.1	1.7	1.3	2.3	3.9	3.8	4.0	1.5	1.2	1.7	2.7	2.3	3.0
	Morehead River	4.2	4.2	4.2	1.4	1.4	1.4	3.9	3.9	3.9	1.3	1.3	1.3	2.3	2.3	2.3
	Kings Plain	4.9	4.6	5.2	1.8	1.7	2.1	3.9	3.9	4.0	1.5	1.4	1.7	2.7	2.5	3.0
Mean		4.7			1.7			3.9			1.5			2.7		
Northern Territory region	Manton River	3.8	3.8	3.8	1.6	1.6	1.6	3.9	3.9	3.9	1.4	1.4	1.4	2.4	2.4	2.4
	Douglas River	3.8	3.4	4.0	1.6	1.1	2.1	3.7	3.7	3.9	1.3	1.2	1.5	2.6	2.4	3.0
	Goomadeer River	3.9	3.2	4.4	1.8	1.7	2.0	3.8	3.8	3.9	1.4	1.3	1.5	2.6	2.4	2.8
	Mann River	4.3	3.9	4.7	1.6	1.5	1.7	3.7	3.7	3.8	1.4	1.2	1.5	2.1	2.0	2.2
	Alligator River	3.6	3.0	4.2	1.5	1.2	1.9	3.7	3.7	3.8	1.3	1.2	1.6	2.4	2.0	2.7
	Elizabeth River	3.8	3.8	3.8	2.6	2.6	2.6	3.8	3.8	3.8	1.5	1.5	1.5	2.8	2.8	2.8
	Melville Island	3.9	3.9	3.9	1.5	1.5	1.5	3.9	3.9	3.9	1.4	1.4	1.4	2.6	2.6	2.6
Mean		3.8			1.7			3.8			1.4			2.5		
Local unimproved trees	Kuiburi	4.4	4.3	4.5	1.6	1.2	2.1	3.8	3.7	3.9	1.4	1.4	1.5	2.9	2.7	3.1
Trial mean		4.3			1.7			3.9			1.5			2.6		
SED region (ANOVA)		0.1			0.1			0.0			0.1			0.1		
SED provenance (ANOVA)		0.3			0.2			0.1			0.1			0.2		
SED family (REML)		0.4			0.2			0.1			0.2			0.2		
h^2		0.11			0.20			-			0.06			0.10		

On a regional basis, trees descended from the original Queensland region generally grew fastest, followed by those from Papua New Guinea, Northern Territory and Thailand (Table 3). The mean height, dbh and tree volume were 11.0 m, 8.7 cm and 235.3 $\times 10^{-4}$ m^3 respectively for Queensland region; 10.3 m, 8.4 cm and 210.2 x 10^{-4} m^3 respectively for Papua New Guinea region; 10.4 m, 7.9 cm and 187.0 $\times 10^{-4}$ m^3 respectively for the Northern Territory region; and 9.4 m, 6.5 cm and 123.2 $\times 10^{-4}$ m^3 respectively for Thailand region. The two local families from an unimproved source showed slower growth, averaging 7.2 m, 4.7 cm and 57.2 $\times 10^{-4}$ m^3 for height, dbh and tree volume respectively.

The differences between provenance origins within regions were less pronounced, compared with those between regions and between families within provenance origins (Table 3). The provenance mean data in Table 3 show that provenance origins within the Northern Territory region were more variable in all growth parameters. In this region, tree volume ranged from 116.3 $\times 10^{-4}$ m^3 for the poorest provenance origin (Melville Island) to 244.2 $\times 10^{-4}$ m^3 for the best provenance origin (Mann River). The ranges were smaller within other regions, i.e. 208.8 $\times 10^{-4}$ – 217.3 $\times 10^{-4}$ m^3 for Papua New Guinea region and 217.0 $\times 10^{-4}$ – 280.7 $\times 10^{-4}$ m^3 for Queensland region.

The best family overall in the trial, descended on at least the maternal side from Kings Plain provenance in Queensland, had a mean individual tree volume of 300.9 $\times 10^{-4}$ m^3 while that of the poorest family was from the local unimproved land race, which produced only 56.8 $\times 10^{-4}$ m^3. All families maternally descended from the Thai candidate plus trees were far below the trial mean in individual tree volume; even the best family measured only 150.8 $\times 10^{-4}$ m^3 compared with 198.1 $\times 10^{-4}$ m^3 of the overall trial mean.

Stem form and branching habit

Genetically-based differences in the stem form and branching habit were evident (Table 2). Regional differences were significant for axis persistence, presence of upright branches and repeated forking while provenance differences were significant only for branch thickness. Differences between families within provenance origins were generally more evident than those between provenance origins except for one trait (presence of upright branches on the lower part of the stem) which displayed significant ($p < 0.05 - < 0.01$) differences at the family level.

The mean values for axis persistence, stem straightness, presence of upright branches, repeated forking and branch thickness are shown in Table 3. Considering region of origin, families descended maternally from Queensland provenances had the best bole length (as reflected by high scoring in axis persistence, region mean 4.7) and were often without upright branches on the lower part of the stem (mean score 3.9). Papua New Guinea region ranked second in axis persistence (mean score 4.4) and presence of upright branches (3.9). Families descended maternally from Northern Territory provenances performed poorly in these respects. Thai and Northern Territory origins scored lower for repeated forking and presence of upright branches (mean 1.4 and 3.8 respectively) compared with Queensland and Papua New Guinea origins (mean 1.5 and 3.9 respectively).

Heritability

Estimates of individual-tree, narrow-sense heritabilities for most parameters were low, but statistically significant, with values of 0.11 for height, 0.14 for dbh, 0.16 for stem volume, 0.11 for axis persistence, 0.20 for stem straightness, 0.06 for repeated forking and 0.10 for branch thickness. The exception was presence of upright branches, for which heritability was not significant.

Discussion

This study clearly indicated a considerable improvement in the growth of *A. auriculiformis* in the second-generation open-pollinated progeny trial. The seed from the first-generation seedling seed orchard greatly out-performed that from a local unimproved stand. Even the poorest-performing provenance origin descended from a natural provenance (Melville Island in Northern Territory) still produced a tree volume (116.3 $\times 10^{-4} m^3$) which was twice that of the local unimproved families (57.2 $\times 10^{-4} m^3$). Trees maternally descended from Queensland provenances were most vigorous, followed by those from Papua New Guinea and Northern Territory. Despite a significant increase in growth rate over local unimproved trees, the Thai selections were out-performed by families descended maternally from Australian and Papua New Guinea provenances. The inferior growth of Thai selections compared with introduced natural populations from Australia and Papua New Guinea was also observed in the first-generation progeny trials (Luangviriyasaeng *et al.* 1995). Since the first introduction of this species to Thailand in 1935, there were no records of further imports of seed until mid 1980s. It is likely that a high degree of inbreeding had built up over many generations. Negative selection, with seed collection from trees having low, easily accessed seed-bearing branches, might also have contributed to its genetic deterioration. The results suggested that the local Thai land race was not a suitable source of genetic material for the breeding program in Thailand. Additional imports focusing on selected provenances in Australia and Papua New Guinea are recommended to augment the genetic base of these provenances already established.

Families descended from Queensland provenances generally had the best stem form. The families from Kings Plain provenance in Queensland were outstanding in most growth parameters. These families were noted not only for fast growth but also for high frequency of single-stemmed trees with a good clear bole, as shown by high scoring for axis persistence and low frequency of upright branches on the lower part of the stem. This particular provenance has performed well in provenance trials in many tropical countries (Awang *et al.* 1994).

Provenance trials of *A. auriculiformis* in many countries have shown that Papua New Guinea seed sources generally perform best in terms of growth while Queensland sources are better in stem form (Awang *et al.* 1994, Bernard 1996, Nguyen 2000). In the first-generation progeny trials of *A. auriculiformis* in Thailand, Papua New Guinea provenance also grow faster than Queensland and Northern Territory provenances (Luangviriyasaeng *et al.* 1995). Half of the top 100 best families in terms of growth and stem form comprised families from Papua New Guinea provenance origin. This was reflected in the high proportion of Papua New Guinea families (i.e. 47) represented in the second-generation progeny trials. However, provenance ranking in the second-generation progeny trials was different from that in the first generation. In an earlier report on two-year growth of these second-generation progeny trials, families of Queensland provenance origin are generally faster growing than those of Papua New Guinea provenance origin (Pinyopusarerk *et al.* 1998). The results at age three years as reported here clearly showed that original Queensland families were better in both growth and stem form. A main activity in the improvement program of *A. auriculiformis* was recurrent selection for general combining ability. It appeared that Queensland parents had high general combining ability as shown by the performance of their progenies. A good cross, thus, may be expected if Queensland parents are used. Inter-provenance hybrids, produced by controlled crosses between selected individuals could further increase the genetic gains if outstanding trees in the resulting progenies are vegetatively propagated for clonal forestry or incorporated in seed orchards.

The majority of families had good stem axis persistence and a low frequency of upright branches on the lower part of the stem. This is a major breakthrough for *A. auriculiformis*, a species renowned for multiple-stem characteristics. Most single-stemmed trees in the trial reported here, however, scored poorly for stem straightness, suggesting that more attention is needed for this economically important trait. The moderate heritability of stem straightness (0.20) suggested that substantial improvement in straightness could be achieved by selection and breeding.

The heritabilities obtained for most traits were low but statistically significant, demonstrating the potential for further genetic gain. They did not reflect the additional genetic gains obtainable by selecting between regions. It should be pointed out that the heritability estimates have been calculated differently to those from provenance-progeny trials of progenies collected from a range of natural provenances. Provenance should properly be specified as a fixed effect to account for the different provenances, each having different pollen pools (Williams & Matheson 1994). The 106 families sampled from the first generation SSO at Sakaerat were descended from a range of regions and provenances, but all parent trees were located within a single small seed orchard. However, the differences in flowering phenology between the Northern Territory provenances, which have a flowering peak from August to November, as well as the Papua New Guinea and Queensland provenances, which have a narrower peak from November to December (Jiwarawat *et al.* 1996), meant that Northern Territory trees were largely unable to mate with those from the other two natural provenance regions. The Thai selections at Sakaerat flower heavily, with a flowering peak similar to that of the Northern Territory origins (Jiwarawat pers. comm.). On this basis, we specified region of origin, but not provenance of origin, as a fixed effect in the calculation of heritabilities in the trial at Kuiburi. This did not give a completely satisfactory estimate of heritabilities for use in prediction of genetic gain, as there was flowering overlap and presumably intercrossing between Papua New Guinea and Queensland as well as between Thailand and Northern Territory. Nevertheless, the estimate was considered more accurate than that which would be obtained by dropping the fixed effect region from the statistical model (which would overly inflate heritabilities) or replacing region with provenance (which would underestimate them).

The marked differences in growth traits between and within provenance origins indicated the potential for immediate gains by identifying which families and provenances performed best in Thailand. In the longer term, selection of superior trees and removal of inferior families in the trial will convert it into a second-generation seedling seed orchard. It is proposed to thin to the best tree in each four-tree family plot, then remove all Thai selections, most families from the Northern Territory region and a few each from within the Queensland and Papua New Guinea regions. After conversion by selective thinning, the Kuiburi trial will be able to deliver seed that display a considerable genetic gain in growth and form traits compared with seed from the best natural provenances of the species in Queensland and Papua New Guinea.

Acknowledgements

We thank staff of the Prachuap Khiri Khan Tree Improvement Station for trial establishment and measurement as well as C. Harwood and A. Kalinganire for their comments on an early draft.

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