GENETIC GAIN FROM BREEDING *ACACIA AURICULIFORMIS* IN VIETNAM

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HAI, P. H., HARWOOD, C., KHA, L. D., PINYOPUSARERK, K. & THINH, H. H. 2008. Genetic gain from breeding *Acacia auriculiformis* in Vietnam. Seedlots of *Acacia auriculiformis* collected from a seedling seed orchard (SSO) and an unpedigreed seed production area (SPA) in northern and central Vietnam were compared with a natural-provenance control and a commercial seedlot from Vietnam. Trials were established on lowland sites in central, north-central and northern Vietnam. Four years after planting, overall survival was good to excellent (83–91%). The SSO and SPA seedlots exhibited significantly ($p < 0.001$) greater height, diameter at breast height (dbh) and stem volume per hectare than the natural provenance controls, which in turn significantly outperformed the local commercial seed source. Conical stem volume in $m^3 ha^{-1}$ at age four years averaged across the three trials was 27.7 for a select SSO seedlot, 23.0 for a select SPA seedlot, 22.3 for a routine SSO seedlot, 19.2 for the natural provenance control and 12.1 for the commercial seedlot. The SSO and SPA seedlots had significantly ($p < 0.001$) straighter stems and reduced incidence of stem forking than the natural provenance control, which was in turn superior to the commercial seedlot. Relative performance of the seedlots at the three trial sites was very similar, indicating seedlot-by-environment interaction was of no practical significance. Selected clones of *A. auriculiformis* included in one trial ranked second in height and diameter growth to the select SSO seedlot and displayed the best stem straightness and axis persistence. The increased dbh values of the SSO and SPA seedlots relative to the natural provenance control were consistent with predictions based on genetic parameters derived from the SSO and selection intensities.

Keywords: Growth, seedlot by environment interaction, seed orchard, seed production area, stem straightness

HAI, P. H., HARWOOD, C., KHA, L. D., PINYOPUSARERK, K. &THINH, H. H. 2008. Gandaan genetik daripada pembiakbakaan *Acacia auriculiformis* di Vietnam. Lot biji benih *Acacia auriculiformis* yang dikumpul dari kebun biji benih anak benih (SSO) dan kawasan pengeluaran biji benih tidak berpedigri (SPA) di utara dan tengah Vietnam dibandingkan dengan kawalan provenans asli serta lot biji benih komersial dari Vietnam. Ujian dijalankan di tapak tanah rendah di tengah, utara-tengah dan utara Vietnam. Empat tahun selepas ditanam, kemandirian keseluruhan dikategorikan sebagai baik hingga sangat baik (83–91%). Lot anak benih SSO dan SPA menunjukkan ketinggian, diameter aras dada (dbh) dan isi padu batang yang secara signifikan ($p < 0.001$) lebih baik berbanding kawalan provenans asli. Provenans kawalan pula jauh mengatasi prestasi biji benih komersial. Purata isi padu kon batang dalam unit $m^3 ha^{-1}$ pada usia empat tahun ialah 27.7 bagi lot biji benih SSO terpilih, 23.0 bagi lot biji benih SPA terpilih, 22.3 bagi lot biji benih SSO rutin, 19.2 bagi kawalan provenans asli dan 12.1 bagi lot biji benih komersial. Lot biji benih SSO and SPA mempunyai batang yang lebih lurus dan kejadian pencabangan batang yang lebih rendah secara signifikan ($p < 0.001$) berbanding kawalan provenans asli. Dalam pada itu kawalan provenans asli adalah lebih baik daripada lot biji benih komersial. Performans relatif di ketiga-tiga tapak adalah sama dan ini menunjukkan interaksi biji benih dan persekitaran adalah langsung tidak signifikan. Klon *A. auriculiformis* terpilih yang dimasukkan dalam satu daripada ujian ini menunjukkan pertumbuhan ketinggian dan diameter yang kedua tertinggi selepas lot biji benih SSO tetapi mempunyai kelurusan batang dan keterusan paksi yang terbaik. Peningkatan dbh lot biji benih SSO dan SPA berbanding dengan kawalan provenans asli menepati ramalan berdasarkan parameter genetik yang diterbitkan daripada keamatan SSO dan keamatan pilihan.

INTRODUCTION

Acacia auriculiformis was introduced into Vietnam in the 1960s. The species has proven well-adapted to lowland environments throughout the country and has become important as a plantation species

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(Nghia 2003), especially in the southern parts of Vietnam. It displays adaptability to a wide range of site conditions and produces pulp logs and small sawlogs on rotations as short as 7–10 years. At present, *A. auriculiformis* plantations occupy some 90 000 ha (Nghia 2003), which is about 4.5% of the total area of Vietnam's forest plantations (Binh 2004). This makes *A. auriculiformis* more important in Vietnam than any other acacia taxon, with the exception of the hybrid between *A. mangium* and *A. auriculiformis*, which is deployed via clonal plantations using selected clones (Van Bueren 2004). However, the productivity of *A. auriculiformis* plantations in Vietnam is relatively poor, averaging about 7 m^3 ha^{-1} $year^{-1}$ (Kha 2003). Factors contributing to the low productivity of *A. auriculiformis* in Vietnam include the relatively low soil fertility and shallow soils of most of the available planting land, low silvicultural inputs (low levels of site preparation, weed control and applied fertilizer), slower growth in northern Vietnam associated with lower winter temperatures and the use of planting stock of poor genetic quality.

Acacia auriculiformis occurs naturally in three separate regions, namely, north Queensland (Qld) and the Northern Territory (NT) in Australia and the south-west of Papua New Guinea and adjacent regions of West Papua, Indonesia (PNG). Allozyme studies on progenies of trees collected in natural populations in Queensland and Papua New Guinea (Moran *et al.* 1989) have revealed that the species is predominantly outcrossing, although a subsequent study reported higher levels of selfing in Northern Territory populations (Wickneswari & Norwati 1995). Provenance trials conducted in several countries have indicated substantial genetic variation in growth and stem form, with important difference between the three regions as well as between provenances within regions (Kamis *et al.* 1994). In south Kalimantan, Indonesia, provenances from Queensland and PNG out-performed most of the provenances from the Northern Territory (Otsamo *et al.* 1996). Queensland provenances also displayed the best height and diameter growth in a trial in Malaysia (Nor Aini *et al.* 1994).

Certain Queensland provenances of *A. auriculiformis* also appear to be the best performers in Vietnam. In a provenance trial at Dai Lai in northern Vietnam, Coen River (Qld) was the best provenance of those tested at age nine years (Kha 2003). Data collected from Dai Lai and another provenance trial at Ba Vi in northern Vietnam at age 12 years showed that Mibini (PNG), Coen River (Qld) and Kings Plains (Qld) were the best-performing provenances at both sites, while Manton River (NT) was fast growing at Ba Vi but mid-ranked at Dai Lai. Other provenance trials of *A. auriculiformis* were established in Cam Quy (Ha Tay province, northern Vietnam), Dong Ha (Quang Tri province, Central Vietnam) and Song May (Dong Nai province, southern Vietnam) in the early 1990s. A local seedlot from Dong Nai was included in these trials as a control. In the trial in Song May, the best-performing provenances at five years were Wenlock R. (Qld), Holroyed (Qld) and Morehead River (PNG), while at Cam Quy the best provenances were Holroyed (Qld) and Rifle Creek (Qld). In these three trials the Dong Nai local race of *A. auriculiformis* displayed intermediate to slow performance. The fastest-growing provenances in these trials had tree volumes twice those of the slowest (Kha 2003).

To help improve the productivity of Vietnam's *A. auriculiformis* plantations, the Research Centre for Forest Tree Improvement (RCFTI) of the Forest Science Institute of Vietnam commenced a genetic improvement programme, with support from CSIRO and Swedish forestry agencies. A seedling seed orchard (SSO) at Ba Vi and an unpedigreed seed production area (SPA) at Dong Ha in central Vietnam were established in the mid-1990s. Both the SSO and the SPA now supply seed for operational planting of *A. auriculiformis* in Vietnam. Selected individual-family seedlots from these plantings are contributing to advanced-generation progeny trials in an ongoing breeding programme. Another SSO established in southern Vietnam was felled when the land was re-zoned for industrial purposes, but over 100 of the best individual trees from this SSO were propagated vegetatively and tested in clonal trials at three locations in southern, north-central and northern Vietnam. In these trials major differences between clones in growth and stem straightness were demonstrated, as well as highly significant clone-by-environment interactions in growth traits (Hai *et al.* 2008a).

Despite the large areas of tropical acacia plantations worldwide, there have been few published reports of the level of genetic improvement achieved in acacia breeding programmes. The advantages of realized genetic gain trials in tree breeding programmes were pointed out by Eldridge *et al.* (1993). Well-designed gain trials using large plot size and adequate replication enable accurate detection of small differences in performance between improved material arising from a breeding programme and appropriate controls, such as unimproved natural-provenance seedlots and other seed sources in commercial use. Estimates of genetic gain from progeny trials using small family plots are less precise. Realized genetic gains for growth and stem form traits in three second generation progeny trials that were being developed into seedling seed orchards of *Acacia mangium* in South Kalimantan, Indonesia were reported by Leksono *et al.* (2003). These trials incorporated open pollinated families from first-generation seed orchards and unimproved families from the same natural regions of provenance. Gains were calculated as percentage increase of orchard families relative to unimproved. Twelve months after planting, average realized genetic gain across the three sublines was 3.1, 5.2, 4.2 and 0.5% for height, diameter at breast height (dbh), stem straightness and multi-stemming respectively. The *A. mangium* progeny trial at Bukidonon on Mindanao Island in the Philippines reported by Arnold and Cuevas (2003) tested 40 families from first generation SSOs in Queensland, Australia and 65 families from natural PNG provenances. At age three years the orchard families had, on average, 12% greater stem volume than the wild PNG families, and significantly straighter stems and reduced forking.

Progeny trials of *A. auriculiformis* have provided some estimates of additive genetic variance and heritability for growth and stem form traits. In Thailand, a second-generation SSO displayed within-provenance heritabilities of 0.11 for height, 0.14 for stem dbh, 0.20 for stem straightness and 0.11 for stem axis persistence at age three years (Luangviriyasaeng & Pinyopusarerk 2002). Of the seedlots in this trial collected from a Thai first-generation seed orchard, those from trees of Queensland provenance origin outperformed those originating from PNG and the Northern Territory. Unselected families from the local Thai land race of *A. auriculiformis* compared very poorly to the seed orchard families descended from Queensland, PNG and the Northern Territory, producing only about ¼ of the stem volume of the Queensland-descended trees. This trial did not include natural-provenance controls, so no estimate of the genetic gain from one generation of breeding could be made.

This paper reports on four-year results of three realized genetic gain trials in central and northern Vietnam which compared the growth of seedlots collected from the *A. auriculiformis* SSO at Ba Vi and SPA at Dong Ha, Vietnam with a natural-provenance control seedlot and a commercial seedlot collected in Vietnam from a seed stand of unknown provenance origin. Also tested in one of the trials were selected *A. auriculiformis* clones approved for commercial planting because of their superior performance in trials (Kha 2005). The growth and stem form of the orchard seedlots relative to the natural provenance and commercial controls were examined. The genetic improvement achieved relative to the natural provenance control was compared with that predicted from genetic parameters estimated in the SSO in Vietnam, taking into account the genetic make-up of the SSO and SPA and the selection intensities applying to selection of the improved seedlots that were tested.

MATERIALS AND METHODS

Seedling seed orchard and seed production area details

Seedling seed orchard

The progeny trial/SSO of *A. auriculiformis* established in 1997 at Ba Vi in northern Vietnam tested 140 open-pollinated families from 13 seed sources of *A. auriculiformis* (Kha 2003, Hai *et al.* 2008b). Fifty-nine of the 140 families were from wild trees in natural provenances in Queensland. These provenances were selected as superior on the basis of their growth and stem form in the earlier provenance trials in Vietnam, but the individual seed trees represented were not specially selected in the course of seed collections. Families from natural provenances in the Northern Territory and PNG were not included in the trial. The remaining 81 families were sourced from the best trees in two first-generation SSOs, one in Northern Territory, Australia of PNG origin and the other in Thailand, i.e. the multi-provenance first-generation SSO described by Luangviriyasaeng & Pinyopusarerk (2002).

The SSO was planted initially as a progeny trial with eight replicates of four-tree family plots of all progenies tested, at a stocking of 1667 stems ha^{-1}. Trees inferior in vigour, or with poor stem straightness, were removed in two selective thinnings, the first of which at three years retained the two best trees per plot, and the second at five years retained the single best tree per plot, reducing stocking to about 400 stems ha^{-1}. No families were completely removed from the orchard. Assuming a coefficient of relationship among individuals within open-pollinated families of 0.33, the trial had a within-provenance heritability for dbh of 0.17 at three years, increasing to 0.24 at five years. The coefficient of additive genetic variation for dbh (the additive genetic standard deviation/trial mean × 100%) was 6.7% at three years and 6.8% at five years (Hai *et al.* 2008b). The estimated heritability for stem straightness in this trial at five years was 0.20. The increase in heritability of dbh in this SSO may have been the result of selective thinning following the three-year and five-year assessments.

Levels of out-crossing in the seed orchard were estimated by assaying allozyme variation in 20 newly-germinated seedlings from each of twelve trees in the orchard, using seed collected in 2002. The mean multi-locus out-crossing rate was 89% (M. W. McDonald, personal communication), indicating that seedlots from the SSO used in the genetic gain trials reported here were predominantly outcrossed, and justifying the coefficient of relationship of 0.33 used to calculate heritabilities (Falconer & Mackay 1996).

Seed production area

In 1996, an unpedigreed seed production area (SPA) was established at Dong Ha in central Vietnam, using a single bulk seedlot. This comprised seed in approximately equal quantities per tree from a total of over 200 parent trees, including natural provenances of *A. auriculiformis* from PNG and Queensland known to be above average in their performances in Vietnam, and trees from the Australian and Thai SSOs previously described as being represented in the SSO. Approximately 60% of the total seed weight was from the natural provenances and 40% was from the SSOs. This SPA was established at an initial stocking of 1200 stems ha^{-1} and was developed into an SPA via two selective thinnings in 1998 and 2000, each thinning removing phenotypically inferior trees of poor vigour and stem form. This thinning reduced stocking at the time of seed collection in the SPA to 400 stems ha^{-1}.

Seedlots tested in genetic gain trials

Table 1 summarizes the genetic treatments tested in the three genetic gain trials. The SSO select seedlot was a seed mix comprising equal quantities of seeds from the best 20 trees per hectare, including only trees from the best 10 families (ranked on an index combining growth and stem form). Thus, selection intensity in standard deviation units (Becker 1992) for this seedlot was approximately 2.6 on the maternal side and 400/1667 (= 1.3) on the paternal side. The SSO routine seedlot comprised seeds from 30 trees of average growth and stem form. Selection intensity was approximately 1.3 on both the maternal and paternal side.

The SPA select seedlot comprised seeds from the phenotypically best trees in the SPA, selected for a combination of growth and stem form. Thus selection intensity on the maternal side was approximately 20/1200 (= 2.5) and on the paternal side was 400/1200 (1.1).

The natural provenance control was a mix of individual-tree seedlots collected from four provenances known to have performed well in previous trials in Vietnam, namely, Coen River, Morehead River and Kings Plains (Qld) and Mibini (PNG). Equal weights of seeds from a total of 31 mother trees from the four provenances were mixed to comprise the bulk, as shown in Table 1.

The commercial control seedlot was obtained from the National Forest Seed Company of Vietnam in 2002. It is considered to be representative of commercial *A. auriculiformis* seed sold in Vietnam at low price. The provenance origin and subsequent genetic history of the stand or stands from which this bulk seedlot was collected are not known.

Four *A. auriculiformis* clones developed from ortets selected by RCFTI in plantings of the Coen River (Qld) provenance at Ba Vi, Vietnam were also included as a treatment in one trial. They were represented as a mix of equal quantities of ramets of the four clones, without retention of clone identities in the field. These clones had previously been tested in a field trial at Dong Ha, central Vietnam. At age 4 years 9 months, mean

Table 1 Genetic treatments tested in realized genetic gain trials of *Acacia auriculiformis* in Vietnam

Treatment	Details	
(1) SSO select	Bulk seedlot of seed from superior individual trees from Ba Vi SSO. The best 20 trees per hectare were selected from among trees of the top 10 families, based on family performance of stem volume and stem straightness.	
(2) SPA select	Bulk seedlot of the phenotypically best 20 individual trees per hectare from the Dong Ha SPA, selected for superior volume and stem form	
(3) SSO routine	Bulk seedlot of 30 trees with average growth rate from the Ba Vi SSO	
(4) Natural provenance	Original provenance seedlot from Australia comprised of equal weights of 31 individual parent trees from four provenances as follows	
	CSIRO 19253 (Kings Plain Lake, Qld)	7 trees
	CSIRO 19250 (Coen R, Qld)	9 trees
	CSIRO 19251 (Morehead R, Qld)	4 trees
	CSIRO 18924 (Mibini, PNG)	11 trees
(5) Commercial	Commercial seedlot from the National Forest Seed Company. Original provenance origin not known.	
(6) Clone mix	Mix of equal numbers of ramets of four selected RCFTI clones (RCFTI clone numbers 81, 83, 84 and 85)	

Qld = Queensland; PNG = Papua New Guinea

stem dbh of the four clones ranged from 9.5 to 11.3 cm, while mean dbh of a control treatment of seedlings of the Coen River (Qld) natural provenance was 8.5 cm (Kha 2005). These clones have been certified for operational planting by a regulation of the Vietnamese Ministry for Agriculture and Rural Development.

Trial locations and site details

Experimental site condition, experimental designs, site preparation and fertilizer applications in the genetic gain trials are described in Table 2. The three trials were planted during the rainy season of 2002. Planting materials were three-month-old seedlings and clonal ramets derived from rooted stem cuttings. These were raised in polythene bags in a soil-based potting mixture. All trials used randomized complete block designs with five replicates and 7 × 7 block plots of each genetic treatment, planted at a spacing of 3 × 3 m. External perimeter rows did not extend fully around the trials, although the trials at Dong Ha and Ba Vi were contiguous with *A. auriculiformis* plantations of the same age on one or two sides of the trial.

Soils at the three trial sites were similar, being relatively shallow infertile, acidic (pH 3.5–4.5) ferralitic clay loams (Chieu & Thuan 1996) and are considered representative of the soils available for planting tropical acacias in northern and central Vietnam. Prior to establishment, sites were cleared and burned and planting holes 30 × 30 × 30 cm in size were cultivated. Well-composted cow manure (2 kg) and NPK fertilizer (0.1 kg) were mixed into the soil of each planting hole before planting. Trials were weeded by hand twice per year for the first two years after establishment.

Assessments

Total tree height (m), dbh (cm), stem straightness and axis persistence of all trees were recorded at age four years. Stem straightness was scored using a scale with five classes:

1: for a very crooked stem with > two serious bends
2: for crooked stem with two serious bends
3: for slightly crooked stem with one serious and/or > two small bends
4: for almost straight stem with one to two small bends
5: for a perfectly straight stem.

Stem axis persistence was scored using a scale with six classes:

1: stem forks at ground level
2: stem forks in first quarter of total tree height

Table 2 Site information for *A. auriculiformis* realized genetic gain trials

	Ba Vi	Dong Hoi	Dong Ha
Latitude	21° 07' N	17° 28' N	16° 50' N
Longitude	105° 26' E	106° 59' E	107° 05' E
Altitude	60 m	40 m	50 m
Soil type	Stony ferralitic clay loam with heavy lateritization	Ferralitic clay loam	Ferralitic clay loam
Annual rainfall (mm)	1680	2370	2370
Annual average temperature (°C)	23	25	25
Planting time	August 2002	November 2002	August 2002
Design	RCBD*	RCBD	RCBD
Replicates	5	5	5
Trees per plot	49 (7 × 7 block plots)	49 (7 × 7 block plots)	49 (7 × 7 block plots)
Spacing	3 × 3 m	3 × 3 m	3 × 3 m
Genetic treatments tested	1–5	1–6	1–5

*RCBD = Randomized complete block design

3: stem forks in second quarter of total tree height
4: stem forks in third quarter of total tree height
5: stem forks in fourth quarter of total tree height
6: single stem persists to the top of the tree

where forking is defined as the presence of a second leader with more than half the diameter of the main leader.

The conical stem volume over bark of each tree was calculated using the following formula:

$$\text{conical volume} = \pi \times \text{height} \times \text{dbh}^2/12 \quad (1)$$

where height is in dm, dbh is in dm and conical volume is in dm^3.

Edge effects were already evident with trees in the outer rows of edge plots in the trials having visibly larger dbh. For this reason, all further analysis was restricted to the net plots, i.e. the inner 5 × 5 trees of each 7 × 7 block plot. Survival was calculated as the percentage of trees surviving in each net plot. Conical stem volume in each net plot was calculated by summing the individual conical volumes of all surviving trees in the plot and using a net plot area of 225 m^2, expressed on a per-hectare basis.

Statistical analysis

Statistical analysis of height, dbh, stem straightness and axis persistence was carried out on plot mean values. Survival and conical volume per hectare were analysed using the values for each net plot. Univariate analyses of all measurements were first carried out for individual sites using the following linear model:

$$Y = \mu + \text{REPL} + \text{SEEDLOT} + \text{ERROR} \quad (2)$$

where
Y = vector of plot observations
μ = site mean
REPL = vector of replicate effects
SEEDLOT = vector of fixed genetic treatment effects
ERROR = vector of residual effects remaining after fitting the model.

Plots of residuals versus fitted values were examined for outliers and to determine whether transformations were required. An arcsin transformation of survival was carried out to improve the distribution of residuals. Analysis was performed using the ANOVA directive in the statistical software package Genstat Release 10 (VSN International Ltd, United Kingdom) with REPL set as a blocking factor and SEEDLOT as a treatment factor.

For each variate, the homogeneity of variances at the three sites was tested using Bartlett's test, applied to the residuals from the three individual-site analyses (Snedecor & Cochran 1980). Across-site analysis was carried out on a combined data set of plot mean values that excluded the clonal treatment (treatment 6) at Dong Hoi. Since this combined data set was balanced and residual errors for each trait were similar at the three sites, a simple across-site fixed-effects analysis was conducted using the following linear model:

$$Y = \mu + SITE + SEEDLOT + SITE.SEEDLOT + SITE.REPL + ERROR \quad (3)$$

where
μ = overall mean
SITE = vector of fixed effects for site
SITE.REPL = vector of replicates within individual sites.

SITE.REPL was set as a blocking factor using the ANOVA directive in Genstat with SITE, SEEDLOT and SITE.SEEDLOT as treatment factors. As in the individual-site analyses, survival was analyzed using an arcsin transformation to improve the normality of the distribution of residual errors. The seedlot effect was declared as fixed in the model because the seedlots were selected a priori and their rankings and individual performance were of interest, while there was no specific interest in estimating the genetic variance among the small number of seedlots tested (Williams *et al.* 2002).

Predicted genetic gain

The SSO and SPA in Vietnam incorporated a proportion of selected families from first-generation SSOs in Australia and Thailand, in addition to families from superior natural provenances. Based on the 9-year dbh of the orchard and natural provenance seed sources in the SSO, and the numbers of families represented by each seed source (Hai *et al.* 2008b), the mean dbh of the SSO was 3.8% greater than the mean of the superior Queensland natural provenances represented in it. This value of 3.8% was taken as the improvement in genetic merit of the SSO relative to the natural provenance control, and a corresponding value of 2.5% was assumed for the SPA, which incorporated a lower proportion of orchard families.

Genetic gain in dbh from selection during thinning and when selecting parents in the SSO and SPA was predicted using the following formula, derived from Falconer and Mackay (1996)

$$\%gain = i \,.\, CV_a \,.\, h \quad (4)$$

where
i = selection intensity in units of standard deviation
CV_a = coefficient of additive genetic variation
h = square root of within-provenance, individual-tree heritability.

Selection intensities on the male and female side in obtaining the SSO and SPA seedlots, based on the thinning and seed collection in the SSO and SPA as described above, were expressed in units of standard deviation (Becker 1992) and averaged (Shelbourne 1992). Coefficients of additive genetic variation and estimates of heritabilities for dbh at three and five years from Hai *et al.* (2008b) were averaged to give values applied to the selective thinning and parental selection in the SSO, and values of these two parameters in the SPA were assumed to be the same.

Gain from the initial compositions of the SSO and SPA and gain from selection of male and female parents were summed to give predicted gain for each of the three SSO and SPA seedlots tested in the genetic gain trials, which could then be compared with the realized gains obtained from the trials.

RESULTS

Survival, growth and stem form at individual sites

The performance of seedlots at the three individual sites is shown in Table 3. Overall survival was good. Genetic treatments differed significantly ($p < 0.05$) in survival only at Dong Hoi, where the clonal treatment displayed lower survival (77.6%) while all seedling treatments had over 90% survival.

Mean growth rates were similar at the three sites, height and dbh being slightly greater at Dong Ha than at the other two sites (Table 3). Genetic treatments differed significantly in their mean height ($p < 0.01$ or $p < 0.001$) and dbh ($p < 0.001$) within each site, with virtually identical treatment rankings at each site. The SSO select seedlot was the best performer at all three sites, followed by the SPA select and SSO

Table 3 Four-year growth, stem straightness, axis persistence and survival of *A. auriculiformis* seedlots in three trials

Site	Seedlot	Height (m)	Dbh (cm)	Conical stem volume (m^3 ha^{-1})	Stem straightness	Axis persistence	Survival (%)
Ba Vi	SSO select	9.97	9.49	24.2	2.91	2.66	88.8
	SPA select	9.38	8.51	18.0	2.87	2.67	84.0
	SSO routine	9.44	8.77	17.8	2.93	2.86	80.0
	Natural provenance	8.71	7.91	14.6	2.80	2.41	83.2
	Commercial	7.87	6.72	9.1	2.62	1.96	76.8
	SED means[1]	0.24	0.24	2.1	0.11	0.13	7.9
	LSD ($p < 0.05$)[2]	0.51	0.51	4.45	0.23	0.28	16.7
	Significant differences[3]	***	***	***	n.s.	***	n.s.
	Site mean	9.07	8.28	16.7	2.83	2.51	82.6
Dong Hoi	SSO select	8.98	10.15	26.1	3.88	4.59	91.2
	SPA select	8.43	9.09	19.8	3.64	4.39	93.6
	SSO routine	8.31	8.77	19.0	3.79	4.33	95.2
	Natural provenance	8.20	8.84	19.2	3.50	3.95	95.2
	Commercial	7.80	7.71	13.4	3.61	3.89	93.6
	Clones	8.76	9.28	18.4	3.95	4.84	77.6
	SED means	0.27	0.36	2.3	0.16	0.24	5.4
	CD ($p < 0.05$)	0.56	0.75	4.80	0.33	0.50	11.26
	Significant differences	***	***	***	n.s.	**	*
	Site mean	8.41	8.97	19.3	3.73	4.33	91.1
Dong Ha	SSO select	10.19	10.73	32.8	3.78	4.30	92.0
	SPA select	9.57	10.45	31.3	3.45	3.83	96.0
	SSO routine	9.70	10.56	30.1	3.35	4.19	89.6
	Natural provenance	8.94	9.49	23.7	3.31	3.70	91.2
	Commercial	7.84	8.25	13.9	3.15	2.30	80.0
	SED means	0.27	0.29	1.8	0.18	0.23	5.4
	CD ($p < 0.05$)	0.57	0.61	3.82	0.38	0.49	11.4
	Significant differences	***	***	***	*	***	n.s
	Site mean	9.25	9.90	26.4	3.41	3.67	89.8

[1] Standard error of difference of treatment means
[2] Least significant difference of treatment means ($p < 0.05$)
[3] Significance of treatment differences: n.s. = not significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

routine seedlots, then the natural provenance control, with the commercial seedlot displaying the slowest growth at all three sites.

Treatment rankings for conical stem volume per hectare were similar to those for height and diameter, although the treatment differences were more pronounced (Table 3). The clonal treatment grew well at Dong Hoi, being ranked second for height and dbh, but because of its lower survival it was ranked fourth for conical volume per hectare, being slightly behind the SPA select and SSO routine seedlots (Table 3).

Stem straightness was poorer at the Ba Vi site, where the site mean for stem straightness score was 2.83, compared with 3.73 at Dong Hoi and 3.41 at Dong Ha (Table 3). Similarly, the axis persistence score was significantly lower at Ba Vi, with a site mean of 2.51 compared with 4.33 at Dong Hoi and 3.67 at Dong Ha. Considering individual sites, seedlots differed significantly ($p < 0.05$) from one another in stem straightness only at Dong Ha, where the ranking of treatments for stem straightness was the same as that for growth traits, SSO select having the best stem straightness and commercial seedlot, the worst. Within-site differences in axis persistence (the height of forking) were significant at all three sites ($p < 0.01$ at Dong Ha and $p < 0.001$ at Ba Vi and Dong Hoi). Within each site, the SSO and SPA seedlots had better axis persistence and straighter stems than the natural provenance control and the commercial seedlot. At Dong Hoi, the clonal treatment displayed the best stem straightness and axis persistence, although it was not significantly superior to the SSO select treatment.

Across-site analysis and seedlot-by-site interaction

For height, dbh and conical volume, residual variances of seedlots 1 to 5 did not differ significantly between sites (chi-square probability for Bartlett's tests for homogeneity of variances > 0.05). Sites did differ in their residual variances for stem straightness ($p < 0.05$) and axis persistence ($p < 0.001$). However, residual mean squares for both stem straightness and axis persistence at the three sites were within a three-fold range. This relative uniformity of residual variation justifies the approach taken for across-site analysis, which assumes a common residual variance across the three sites. Across-site analysis of variance confirmed that there were highly significant ($p < 0.05$) differences between the three sites and also among the five seedlots for four-year height, dbh, conical stem volume per hectare, stem straightness and axis persistence (Table 4). Differences in survival between sites and between the five seed-based seedlots were not significant ($p > 0.05$) (analysis not shown in Table 4). The site-by-seedlot interaction was significant ($p < 0.05$) for height, dbh and conical stem volume per hectare, but the mean square for the interaction was only a very small percentage of the seedlot mean square (less than 6% for height and volume and less than 4% for dbh). Site-by-seedlot interaction was not significant for stem straightness or survival but was highly significant for axis persistence ($p < 0.001$) although it was again relatively small; only 16% of the seedlot mean square for this variate. Clearly, the rankings of seedlots for height, dbh, stem straightness, axis persistence and conical volume per hectare across the three trial sites were relatively stable and site-by-seedlot interaction, while significant for growth traits and axis persistence, was very small compared with the differences between the seedlots. The stability of rankings across sites is illustrated graphically for conical volume in Figure 1.

Considering the average performance of each seedlot at four years across the three sites, conical volumes ($m^3 ha^{-1}$) were 27.7 for the SSO select seedlot, 23.0 for the SPA select, 22.3 for SSO routine, 19.2 for the natural provenance control and 12.1 for the commercial seedlot (Table 5). In comparison with the natural provenance control there was a 45% increase in volume per hectare for the SSO select, 23% for the SPA select and 22% for the SSO routine, whereas the commercial seedlot produced 37% less volume than the control. Corresponding percentage differences in height, dbh, stem straightness and forking indices were less than those for volume (Table 5).

Realized genetic gain compared with predicted gain

The across-site estimates for dbh from Table 5 were taken to represent the genetic gains in dbh at four years obtained from the SSO and SPA seedlots of *A. auriculiformis* tested in the trials. Realized gains in dbh, expressed as percent gain relative to the natural provenance control, were

Table 4 Across-site analysis of variance for growth and stem form traits

Source of variation	d.f.[1]	s.s.[1]	m.s.[1]	v.r.[1]	F pr.[1]
Height					
Replicate stratum					
Site	2	11.511	5.755	7.67	0.007
Residual	12	9.007	0.751	4.71	
Plot stratum					
Seedlot	4	29.831	7.458	46.81	< 0.001
Site.seedlot	8	3.312	0.414	2.6	0.019
Residual	48	7.648	0.159		
Dbh					
Replicate stratum					
Site	2	33.124	16.562	22.25	< 0.001
Residual	12	8.934	0.745	3.76	
Plot stratum					
Seedlot	4	54.712	13.678	69.13	< 0.001
Site.seedlot	8	3.598	0.450	2.27	0.038
Residual	48	9.497	0.198		
Conical stem volume ha^{-1}					
Replicate stratum					
Site	2	1225.2	612.6	13.33	< 0.001
Residual	12	551.3	45.94	4.42	
Plot stratum					
Seedlot	4	1991.24	497.81	47.87	< 0.001
Site.seedlot	8	232.69	29.09	2.8	0.013
Residual	48	499.12	10.4		
Stem straightness					
Replicate stratum					
Site	2	9.556	4.778	18.44	< 0.001
Residual	12	3.109	0.259	4.24	
Plot stratum					
Seedlot	4	1.399	0.350	5.72	< 0.001
Site.seedlot	8	0.477	0.060	0.98	0.467
Residual	48	2.934	0.061		
Axis persistence					
Replicate stratum					
Site	2	38.275	19.138	75.39	< 0.001
Residual	12	3.046	0.254	2.25	
Plot stratum					
Seedlot	4	12.799	3.200	28.38	< 0.001
Site.seedlot	8	4.207	0.526	4.66	< 0.001
Residual	48	5.412	0.113		

[1]d.f = degrees of freedom, s.s. = sum of squares, m.s = mean square, v.r. = variance ratio, F pr. = F probability

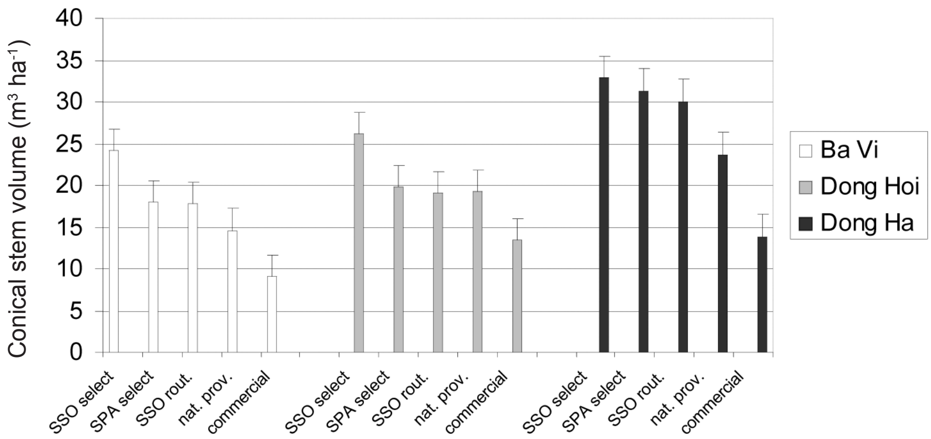

Figure 1 Four-year conical stem volumes per hectare for the *Acacia auriculiformis* seedlots tested in three trials. Error bars show standard error of difference of means.

Table 5 Four-year performance of orchard and commercial seedlots tested across three sites, in absolute and percentage terms, relative to natural provenance control

	SSO select	SPA select	SSO routine	Natural provenance	Commercial
Height (m)	9.72	9.13	9.15	8.62	7.84
Dbh (cm)	10.12	9.35	9.37	8.75	7.56
Conical stem volume (m^3 ha^{-1})	27.70	23.00	22.30	19.20	12.10
Stem straightness (units)	3.53	3.32	3.36	3.20	3.13
Axis persistence (units)	3.85	3.63	3.80	3.35	2.72
Percentage relative to control					
Height	113	106	106	100	91
Dbh	115	107	107	100	87
Conical stem volume	144	120	116	100	63
Stem straightness	110	104	105	100	98
Axis persistence	115	108	113	100	81

15.7% for SSO select, 6.9% for SPA select and 7.1% for SSO routine (Table 5). These realized gains can be compared with the corresponding gains predicted from orchard composition effects, additive genetic variance and selection intensity, which were calculated to be 9.9, 8.0 and 7.7% respectively (Table 6). As expected, the SSO select seedlot outperformed the SSO routine seedlot because of the higher selection intensity on the female side (2.6 versus 1.3, Table 6). The degree of improvement in dbh realized was quite similar to that predicted. A number of factors which affect the estimates of predicted gain are discussed below.

DISCUSSION

Overall performance and realized gain

Trial mean heights of 8 to 9 m at age four years observed in these trials are typical of the performance of *A. auriculiformis* in northern and central Vietnam (Kha 2003). Comparing the performances of seedlots from the Vietnamese SSO and SPA with that of the natural provenance control, significant ($p < 0.05$) realized gain in growth, improved stem straightness and reduced incidence of forking has been achieved.

Table 6 Realized and predicted genetic gain in dbh for *A. auriculiformis*

Seedlot	SSO select	SPA select	SSO routine	Natural provenance
Realized genetic gain:				
Mean dbh (cm) across three trial sites	10.12	9.35	9.37	8.75
Realized gain (%) relative to natural provenance control	15.7	6.9	7.1	100
Predicted genetic gain:				
% predicted gain in dbh of SSO and SPA relative to natural provenances1	3.8	2.5	3.8	
Selection intensity (female side)	2.6	2.5	1.3	
Selection intensity (male side)	1.3	1.1	1.3	
Selection intensity (average of male and female)	2.0	1.8	1.3	
Coefficient of additive genetic variation	6.7	6.7	6.7	
Heritability	0.20	0.20	0.20	
Square root of heritability	0.45	0.45	0.45	
Predicted % gain in dbh from selection of parents in SSO and SPA	6.1	5.5	3.9	
Total predicted % gain in dbh	9.9	8.0	7.7	

[1] Based on superior performance of seed orchard families from Australia and Thailand incorporated in SSO and SPA

Of great concern for growers in Vietnam is the very poor performance of the commercial seedlot, which yielded only 63% of the volume of the natural provenance seed, and also had poorer stem straightness and axis persistence. Growers using the commercial seedlot suffer a heavy penalty in reduced volume at harvest and poorer stem form (poorer stem straightness and axis persistence), leading to lower yields of saleable products. The poor performance of the commercial seedlot is probably the result of a combination of several factors, including (1) initial introduction of suboptimal provenances of *A. auriculiformis* to Vietnam in the 1960s, (2) possible inbreeding during informal domestication, with resulting inbreeding depression of growth (Harwood *et al.* 2004) and (3) preferential seed collection from low, branching trees with easily accessible seed crops, resulting in selection for reduced growth and poor stem form over one or more generations. The slow growth and poor stem form of the Vienamese commercial seedlot is consistent with the poor performance of the land races of *A. auriculiformis* that have developed in Thailand (Luangviriyasaeng & Pinyopusarerk 2002).

Seedlot-by-site interaction

The level of seedlot-by-site interaction, while statistically significant for all traits except stem straightness, was very low, despite the considerable geographic differences and associated climatic differences between the three sites. The southernmost (Dong Ha) and northernmost (Ba Vi) sites are separated by more than 500 km and 4° of latitude, and Ba Vi experiences cooler winters and a lower frequency of typhoons than the other two sites. The ratio of the site-by-seedlot interaction mean square to the seedlot mean square in the across-site analyses (Table 4) ranged from 3 to 6% for the three growth traits and was 16–17% for the two stem form traits, far lower than the 50% level suggested by Shelbourne's (1972) 'rule of thumb' as being likely to cause problems for genetic testing and deployment across a range of sites. Genotype-by-environment interaction can be characterized as two main types, namely, scale change interaction and rank change interaction (White *et al.* 2007). Scale change interaction involves differential performance of genotypes across sites, but no change in performance ranking. Where seedlot rankings change, rank change interaction is present. The implication of rank change interaction is that breeding programme must be specially tailored to produce material for differing site types. This study has identified scale change interaction only, with no substantial rank changes across sites.

Marked rank change interaction may be less likely in experiments where different genotypes are homogenized within broader genetic groupings, such as provenance trials and gain trials from open pollinated seed sources. If different individual genotypes within each seedlot have differing patterns of adaptation across the three sites, seedlot mean performance can mask GxE at the individual genotype level (Namkoong *et al.* 1988). In our study, estimates of performance of each seedlot at each site were based on a large sample of five plots, with up to 25 trees per plot, derived from a mix of 20 or more open-pollinated families, so there was a substantial degree of genetic 'buffering' within each seedlot. The expression of GxE was much more pronounced in clonal trials of *A. auriculiformis* in Vietnam, where the changes in rankings of individual genotypes across contrasting sites could be monitored (Hai *et al.* 2008a). The authors tested 130 clones, most of them selected from a progeny trial in southern Vietnam, in three clone trials that spanned a wider range of environments (the Ha Tay and Dong Hoi locations tested in our trials, and Bau Bang, in the south of Vietnam, latitude 11° N). These trials demonstrated high genotypic heritability for growth traits at three years but low genotypic correlations between sites. The site-site genotypic correlation for 3-year dbh between Ba Vi and Dong Hoi in these clone trials was relatively low at 0.50 ± 0.15, (Hai *et al.* 2008a), indicating that GxE at the clone level was much greater than differences in seedlot performance across these two sites observed in the current study.

Realized genetic gain compared with predicted gain

A number of qualifications apply to the calculation of predicted gain. The initial advantage of the SSO and SPA relative to the natural provenance control seedlots is not known exactly because the natural provenance seedlots represented in the SSO and SPA were somewhat different to those used to comprise the control seedlot used in the gain trials, although some of the provenances were in common. Nonetheless, the chosen advantages of 3.8% for the SSO and 2.5% the SPA are considered realistic (Table 6).

The level of outcrossing in the SSO was found to be high (89%) but that in the SPA was not assessed, and if it differed substantially this would affect SPA seed crop performance. Selection within the SSO and SPA was not for dbh alone but was on a subjective multitrait index combining tree vigour and improved stem form. This would tend to reduce the selection intensity, relative to that resulting from single-trait selection for dbh. However, Hai *et al.* (2008b) reported strong, positive genetic correlations among dbh, stem straightness and axis persistence, so the reduction in selection intensity for dbh was probably only minor. For the SSO select seedlot, the selection intensity on the female side was actually higher, because only female parents from among the 10 best families in the trial were selected; so there was a combination of between family and within-family selection, which would lead to greater gain (Shelbourne 1992). This greater advantage of the SSO select seedlot over the control was in fact observed in the realized gain (Table 6).

Finally, the predictions of gain from selection within the SSO and SPA are complicated by differences between seed sources (the different natural provenances and the Australian and Thai seed orchards) which would increase the additive genetic variance and thus the genetic gain from selection. Given the various uncertainties and simplifying assumptions, the predicted genetic gain in dbh agreed well with the realized gain in dbh, averaged across the three trials.

Implications for genetic improvement strategy

A seed orchard and a seed production area in Vietnam incorporating families from known best natural provenances and some seed orchard families from other countries delivered a substantial degree of genetic gain in growth and stem form traits, relative to a control seedlot which was a mix of four superior natural provenances (Kha 2003). In this study, the SSO and SPA performance is markedly superior to the Vietnamese commercial seedlot. Growers using the SSO select seed would obtain over twice the conical stem volume per hectare. Improved stem form would further increase the volume of saleable sawlog and pulpwood, relative to the commercial seed, which is widely used in Vietnam.

One kilogram of *A. auriculiformis* seed contains about 30 000 seeds. The annual yield of seed from the SSO and SPA, each less than three hectares in size, is only a few kilograms, sufficient only for the establishment of one or two hundred hectares of plantations. Suitable land for establishment of additional seed orchards is very hard to acquire. The most effective route to deliver highly improved planting stock in large quantity to growers in Vietnam will be clonal propagation of elite field-tested clones, now available from the clonal testing programme. The four clones tested in the Dong Hoi trial are ranked lower than many of the clones tested by Hai *et al.* (2008a). Clonal propagation of selected *Acacia* hybrid clones in Vietnam has enabled establishment of over 150 000 ha of *Acacia* hybrid plantations within a few years (Van Bueren 2004). However, an ongoing breeding programme for *A. auriculiformis* is clearly justified to deliver further genetic improvement and progressively better clones as well as improved parents for the hybrid breeding programme.

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