Genetic Improvement of Plantation-Grown *Acacia auriculiformis* for Sawn Timber Production

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Cover: Intensively managed 3-year-old plantation of *Acacia auriculiformis* in Vietnam
(Photo: Phi Hong Hai)

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Abstract

Breeding of *Acacia auriculiformis* A.Cunn. ex Benth in Vietnam, which commenced in 1996, has focused to date on improving tree growth and stem straightness. Little attention has been paid to important properties of wood such as basic density, shrinkage, bending stiffness and strength, which determine suitability for specific end-use applications. The aim of the studies reported here was to obtain knowledge of genetic factors associated with wood traits and their relationships with growth and tree form, in order to facilitate improvement of *A. auriculiformis* for sawn timber production.

Empirical data were gathered in a progeny test, three clonal tests and three genetic gain tests in four provinces of Vietnam. Genetic parameters for the studied traits were estimated at ages ranging from 3 to 9 years. The results showed that individual within-provenance heritabilities (h^2) and clonal repeatabilities (H^2) for growth, stem straightness, basic density and shrinkage increased with age, but those for mechanical properties were stable with age. In the progeny test, h^2 ranged from 0.36 to 0.39 for growth traits, 0.40-0.61 for density and 0.12–0.31 for stem straightness. In clonal tests, H^2 ranged from 0.21 to 0.56 for growth traits, 0.16-0.38 for shrinkage traits, and 0.21-0.57 for mechanical properties. Growth and wood properties had coefficients of additive genetic variation (CV_A) and genotypic variation (CV_G) ranging from 5-12%. High age-age correlations for most studied traits were found, suggesting that there would be more gain per unit time by selecting trees at 3 to 4 years old than at greater ages. Growth traits showed consistent positive genetic correlations with stem straightness, but non-significant correlations with wood properties, except for a significant negative correlation between diameter and stiffness. Genotype by environment interaction was important for growth and stem straightness in clone trials across southern, central-north and northern Vietnam, but not important for a number of improved and unimproved seedlots compared in genetic gain trials across northern, central-north and central Vietnam. Predicted and realised gains for growth were substantial for seed orchard seedlots produced by the current breeding program, compared with natural-provenance and local commercial control seedlots. Good gains in growth and form traits and wood properties could be obtained from clonal selection, although the absence of strong, favourable correlations between growth and wood properties indicates that gains for individual traits would be reduced if a multi-trait improvement approach was adopted.

The findings clearly demonstrate that there is potential to improve tree growth, stem straightness, wood density, shrinkage and mechanical properties of *A. auriculiformis* in Vietnam.

Keyword: *Acacia auriculiformis*, correlated response, genetic correlation, genotype by environment interaction, genetic gain, heritability, sawn timber, wood property

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Dedication

To my family

Contents

List of Publications

This thesis is based on the following papers, which will be referred to by the corresponding Roman numerals:

I Hai, P.H., Jansson, G., Harwood, C., Hannrup, B. & Thinh, H.H. (2008). Genetic variation in growth, stem straightness and branch thickness in clonal trials of *Acacia auriculiformis* at three contrasting sites in Vietnam. *Forest Ecology and Management* 255(1), 156-167.

II Hai, P.H., Jansson, G., Harwood, C., Hannrup, B., Thinh, H.H. & Pinyopusarerk, K. (2008). Genetic variation in wood basic density and knot index and their relationship with growth traits for *Acacia auriculiformis* A. Cunn ex Benth in Northern Vietnam. *New Zealand Journal of Forestry Science* 38(1), 176-192.

III Hai, P.H., Jansson, G., Hannrup, B., Harwood, C. & Thinh, H.H. (2009). Use of wood shrinkage characteristics in breeding of fast-grown *Acacia auriculiformis* A. Cunn. ex Benth in Vietnam. *Annals of Forest Science* 66 (6), 611p1-611p9.

IV Hai, P.H., Hannrup, B., Harwood, C., Jansson, G. & Ban, D. V. (2009). Wood stiffness and strength as selection traits for sawn timber in *Acacia auriculiformis* A. Cunn. ex Benth. (Submitted).

V Hai, P.H., Harwood, C., Kha, L.D., Pinyopusarerk, K. & Thinh, H.H. (2008). Genetic gain from breeding *Acacia auriculiformis* in Vietnam. *Journal of Tropical Forest Science* 20(4), 313-327.

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1 Introduction

The Vietnamese Government is currently striving to establish plantations of fast-growing trees in order to ensure adequate wood supplies for the existing wood-based industries in the country. The results from international trials of *Acacia* species and provenances (Kha, 2003; Luangviriyasaeng & Pinyopusarerk, 2002; Nor Aini *et al.*, 1994; Yang & Zeng, 1991) have shown that *Acacia auriculiformis* is a useful multi-purpose tree species, being fast-growing and suitable for timber and pulp production (Nghia, 2003; Turnbull *et al.*, 1997). The species was introduced into Vietnam in the 1960s. It has proven to be well-adapted to lowland environments throughout Vietnam and has become an important plantation species (Nghia, 2003). It is adaptable to a wide range of site conditions and produces pulp logs and small sawlogs in rotations as short as 7-10 years. *Acacia auriculiformis* plantations currently occupy some 71,600 ha (Ministry of Agriculture and Rural Development, 2007), equivalent to ca. 4% of the total area of Vietnam's forest plantations. This makes *A. auriculiformis* more important in Vietnam than any other *Acacia* species, with the exception of the hybrid between *A. mangium* and *A. auriculiformis* (van Bueren, 2004).

The goal of most modern tree improvement programs is to combine rapid stem volume growth with improved stem straightness and desired wood properties, so as to produce well-adapted trees capable of supplying high-quality logs for both lumber and pulpwood (Doede & Adams, 1998; Zobel & Talbert, 1984). Wood density, shrinkage and stiffness are often considered the most important wood traits, because of their effects on wood recovery and nearly all final products of sawn timber (Raymond, 2002; Zobel & Van Buijtenen, 1989; Bendtsen, 1978).

Juvenile wood is defined in various ways by different authors (Zobel & Sprague 1998; Walker, 2006), but it is commonly understood to comprise the first few annual rings of wood laid down around the pith, and in the first few metres from the base of the tree. Burdon *et al.* (2004) describe the radial changes that occur in wood properties as a transition from corewood to outerwood, and the longitudinal change in wood properties as a transition from juvenile to mature wood. Fast-grown plantation logs in Vietnam, harvested at ages of 10 years or less, can be effectively considered as consisting entirely of juvenile wood. Since juvenile wood will be used increasingly in the future, there is a need for research on genetic variations in juvenile wood properties, their correlations with tree growth and their impact on end-use products (Zobel & Sprague, 1998; Rozenberg & Cahalan, 1997).

Clonal forestry, the mass-production via vegetative propagation of improved planting stock of tested clones, has been promoted as an alternative to the use of genetically improved seed produced in seed orchards. There are many advantages of clonal forestry, including the opportunities to capture both additive and non-additive genetic effects, which should result in larger gains from selection than can be obtained using sexually produced offspring (Libby & Rauter, 1984). Developing clonal forestry for *A. auriculiformis* requires estimation of genotypic parameters, in order to determine the best strategy for clonal testing and deployment. Knowledge of genotype by environment interactions is also needed to design testing, selection and deployment procedures in any breeding program (Namkoong, 1981; Burdon, 1977).

Therefore, the studies in this thesis are based upon addressed genetic variations in economically important traits of *A. auriculiformis*, including growth traits, stem straightness, branching patterns, and wood properties (wood basic density, shrinkage, stiffness and strength). The genetic relationships between wood properties and growth traits were also examined. The results obtained, and their implications for the development of a breeding and deployment program of the species for sawn timber production, are considered below.

1.1 Wood demand and use

There is globally increasing demand for high value solid hardwood products that have been traditionally sourced from native forests. As a result of unsustainable logging practices in the past, increased environmental awareness and the need to expand in the area of conservation and rehabilitation forests, the availability of native forests as sawlog resources is rapidly diminishing (Barnett & Jeronimidis, 2003). Coinciding with the reduced access to native forests for logging in the tropics and subtropics, there has been rapid expansion in short rotation hardwood plantations as sources of both short-fibre pulp and raw materials to replace solid-wood products of native forests. These factors are all of particular relevance in Vietnam, where there is a large human population, a high demand for saw-lumber and a high proportion of native forests protected from logging.

Vietnam's total wood (lumber and pulp wood) production increased from 2,122,000 in 1999 to 2,703,000 metric tonnes in 2005, mostly due to an increase in wood production from plantations (Dao, 2006). However, wood imports have increased dramatically over the last eight years, by almost 6-fold since 2000, Vietnam's wood processing industry imported 80% of the wood materials it used in the period 1999-2005 (Dao, 2006), and as the furniture-manufacturing sector continues to expand the demand for wood is expected to keep on growing.

Plantation-grown *A. auriculiformis* trees have been found to be very promising for the production of unbleached kraft pulp and high quality neutral sulphite semichemical pulp (Pinyopusarerk, 1990). Therefore, small logs of *A. auriculiformis* have been used for making pulp and paper in Vietnam, and have been exported as wood chips to other countries. However, logs of sufficient size (typically with small-end diameters of at least 15 cm) fetch higher prices when sold as sawlogs, because of the high demand from Vietnam's wood-processing industries. The wood of *A. auriculiformis* is known to be very attractive for furniture, wood turning and carving as well as being suitable for construction work, e.g. framing and flooring (Pinyopusarerk, 1990). Consequently, there has been a particular focus in Vietnam on growing the species for higher value end-uses. An increasing area of *A. auriculiformis* plantations is now managed for the production of saw and veneer logs, especially in the south of Vietnam.

1.2 Natural distribution and biology of *A. auriculiformis*

The 1300 species of the genus *Acacia* extend around the globe, from Australia, through Asia to Africa and the Americas. These insect-pollinated, nitrogen-fixing trees grow in a range of environments and fill an important niche in natural ecosystems. They have also been planted as exotics in over 70 countries, for land rehabilitation and to produce a range of wood and non-wood products, and fodder (Turnbull *et al.*, 1997).

Acacia auriculiformis occurs naturally in Australia, Papua New Guinea (PNG) and Indonesia (Figure 1), between latitudes 9-16^{0}S and longitudes 130-145^{0}E. The altitudinal range of species in its native range is from sea level to about 400 m. Climatically, *A. auriculiformis* occurs in hot humid and subhumid zones, where the mean maximum temperature of the warmest month is 32-38^{0}C and the mean minimum temperature of the coldest month is 12-20^{0}C. Frosts do not occur in the species' natural range, and annual rainfall varies from 760 mm to 2000 mm. *Acacia auriculiformis* grows in a wide range of soils with a pH range from 4.0 to 9.0 (Pinyopusarerk, 1990).

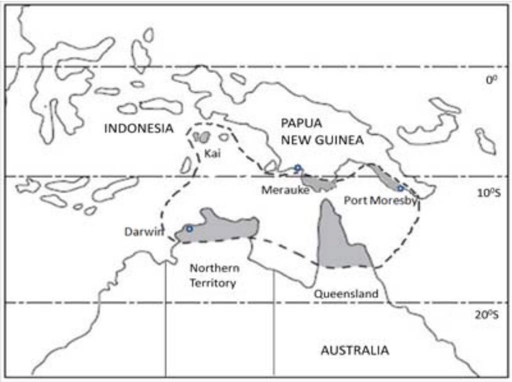

Figure 1. Natural distribution of *A. auriculiformis*, adapted from *(Pinyopusarerk, 1990).*

Acacia auriculiformis is a fast growing, small to medium-size tree species, generally reaching heights of 8 to 20 m, heavily branched with a short, crooked stem, but on some favourable sites it can grow to 30 m tall and 80 cm in diameter with a straight, single stem (Pinyopusarerk, 1990). The species possesses wood properties that are suitable for a wide range of uses. The wood is heavy, with a high percentage of heartwood that is quite durable. The heartwood is light brown to dark red in colour and straight-grained. The texture is fine to medium and basic density is between 500-800 kg m^{-3}. The wood fibres are relatively short, about 1.1 mm in long and 20.6 µm in wide (Jahan *et al.*, 2008). The wood basic density, bending stiffness and strength are considered to be high and compare well with those of teak (*Tectona grandis*). The wood is easy to work, takes a good polish and finishes well with sharp tools. However, the boards tend to split when sawn. With regard to chemical composition, the wood's α-cellulose, hemicellulose, lignin and extractives contents are ca. 44.1%, 32%, 19.4% and 4.5%, respectively (Jahan *et al.*, 2008).

Allozyme studies on progenies of *A. auriculiformis* trees collected in natural populations in Queensland (Qld) and Papua New Guinea (PNG) (Moran *et al.*, 1989) have revealed that the species is predominantly outcrossing, although a subsequent study reported higher levels of selfing in Northern Territory (NT) populations (Wickneswari & Norwati, 1993).

There are very few tree species that are as adaptable as *A. auriculiformis* (Pinyopusarerk, 1990). It grows well in a wide range of environmental conditions in the tropics and has proven to be especially suitable for rehabilitating and revegetating difficult sites in Asian countries. By the mid-1990s, the total plantation area of the species was estimated to have reached 60,000 ha in China, 45,000 ha in India, and less than 10,000 ha in other countries such as Thailand, Philippines, Indonesia and Malaysia (Turnbull *et al.*, 1997).

1.3 The current status of *A. auriculiformis* breeding in Vietnam

Provenance trials have been established since the 1980s in several parts of Vietnam. Highly significant differences between provenances have been reported for growth rate and stem straightness. Mibini (PNG), Coen River (Qld), Kings Plains (Qld), Wenlock R. (Qld), Halroyed (Qld) and Morehead (PNG) were the best performing provenances in Vietnam (Kha, 2003). Significant improvements in plantations are therefore possible, simply by using selected provenances (Kha, 2003; Nghia, 2003). In addition to investigations of *Acacia* species, natural acacia hybrids have been studied since 1993 (van Bueren, 2004), and the development of hybrid clones of *A. mangium* and *A. auriculiformis* has recently been given high priority by breeders in Vietnam. The morphology and wood density of F_1 *A. auriculiformis* x *A. mangium* hybrids has been found to be intermediate between those of the parental species, but clear heterosis in growth rates has been observed (Kha, 2001). Outstanding hybrid clones have been identified, tested and are now being mass propagated for operational clonal forestry (Kha, 2001), with over 220,000 ha of clonal plantations established to date.

For long-term breeding, a program to improve *A. auriculiformis* trees growing under Vietnamese conditions was started in 1996. Several progeny tests and clonal tests were established, in order to develop a comprehensive genetic base population for breeding, establish seed orchards, generate tested clones for production forestry and provide information on genetic variation and the potential for continued genetic improvement. Two provenance-progeny trials testing a total of 203 open-pollinated families from 13 provenances were established in the breeding program. This base population for breeding was compromised in 1999, because land in Binh Duong, where the larger first-generation progeny test was located, was assigned to other uses and the progeny trial was lost. However, before the trial was felled, 150 superior individual trees within 65 families were selected from the Binh Duong progeny test, based on individual tree performance for growth and stem straightness. These selected trees were clonally propagated and used for establishing three clonal tests in the north, central-north and south of Vietnam.

Knowledge of genetic parameters, such as coefficients of variation, heritabilities, genetic correlations, genotype by environment (G × E) interactions, and predicted gains, realised gains for traits of interest, as well as correlated responses, are essential for implementing a breeding program. This information was obtained from studying the genetic trials of *A. auriculiformis* in Vietnam and forms the basis of this thesis.

1.4 Economically important properties for sawn timber

Breeding objectives need to be based on clear definitions of the key economic parameters driving the production system. The key economic drivers commonly identified for sawn timber are green sawn recovery, dimensional stability, timber strength, drying degrade and durability (Raymond, 2002; Raymond, 2000). The relationships between the tree, log and wood traits considered in this thesis and these determinants of processing profitability, as well as their strength of genetic control, are summarized in Table 1 and discussed below.

Log diameter, stem straightness and branching patterns

The diameter of the log is most important to the miller (Steele, 1984). Generally, large diameter logs give greater sawn timber recovery, at lower fixed milling costs with a greater proportion of timber achieving the higher value grades (Walker, 2006). Larger logs are also easier to quarter-saw and may be less prone to growth stress problems (Steele, 1984). Larger dimension boards can only be cut from large diameter logs.

Two of the easiest traits to target in attempts to improve trees for sawn wood production are stem straightness and branching patterns, because of their effects on wood quality and clear-wood volume production, moderate heritability and ease of measurement, compared with wood traits (Zobel & Jett, 1995). Straight trees produce less tension wood and provide higher yields of sawn timber than bent trees of similar size. Therefore, stem straightness has been one of the main parameters targeted in breeding strategies for industrial wood production. Small limbs and high branch angles are two other important traits targeted in tree breeding programs for solid wood production, partly because small branches with large branch angles to the main stem (i.e. close-to-horizontal branches) leave small wounds when pruned, which have been shown to less heavily affected by microbial infections than large wounds, at least in *Eucalyptus nitens* wood (Pinkard, 2002). Usually, stem straightness and branching patterns are

Table 1. The relationships between key selection properties and key economic drivers, the importance of selection properties for various solid wood products and strength of genetic control of the key selection properties. Adapted from Raymond (2000).

Key selection property	Economic drivers					Solid wood products			Heritability
	Green sawn recovery	Timber strength	Dimensional stability	Drying degrade	Durability	Furniture	Flooring	Structural	
Large log diameter	x	x	x	x	x	high	high	high	low-moderate
Stem straightness	x					high	high	high	low
Small branches	x	x	x	x		high	high	medium	low
Knot size	x	x	x	x		high	high	medium	low
Basic density	x	x	x	x	x	medium	high	high	high
Density gradient	x	x	x	x		high	high	high	moderate
Shrinkage			x	x		high	high	high	moderate
Modulus of rupture		x				high	high	high	moderate
Modulus of elasticity		x				high	high	high	moderate

Notes: x = indicates the important wood properties for particular solid wood product; Heritability estimates are ranked: high, moderate and low refer to heritabilities > 0.4, 0.2 to 0.4, and < 0.2, respectively.

assessed on a qualitative scale (i.e. using a visual point scoring method) (Cotterill & Dean, 1990).

Wood basic density

Wood basic density is expressed as oven-dry weight per unit green volume, measured in g cm^{-3} or kg m^{-3}. Wood density is one of the most important traits to consider in solid wood production, because of its key importance in forest product manufacture (Rozenberg & Cahalan, 1997). Density has positive relationships with desirable mechanical properties of wood (Evans & Ilic, 2001; Zobel & Jett, 1995; Hillis & Brown, 1984). It is also positively correlated with the shrinking and swelling parameters of wood, but less directly than with mechanical properties (Barnett & Jeronimidis, 2003). Structural timber needs high density and strength, while low-density wood may be more suitable for pulp and paper products than for construction (Barnett & Jeronimidis, 2003). Wood with density in the range of 470-550 kg m^{-3} is well suited for pulp production (Dean, 1995).

Wood density is a complex physical property, since wood tissue is composed of varying proportions of wood cells and chemicals (Zobel & Jett, 1995). Consequently, a change in one or more cell types in the wood, and/or in chemical composition, could change the overall density. Further, wood density is related to wood porosity; the lower the void volume and the thicker the cell walls of the wood, the higher the wood density (Walker, 2006).

Radial variation in density

The difficulty of measuring variations in radial density (which can be thought of as the variation in density from pith to bark) has impeded the use of this trait in breeding programs in the past (Zobel & Jett, 1995; Wright & Burley, 1990). A low pith-to-bark density gradient is important in both earlywood and latewood for maximising solid wood product recovery, because of the strong relationships between density and both wood strength and shrinkage parameters (Malan, 1997). Variations in radial density are therefore linked to radial changes in strength and shrinkage traits. This has been widely recognized as contributing to various processing problems (Walker, 2006), such as warping of timber, but such relationships have not been widely reported (Yang & Fife, 2003).

Shrinkage

Shrinkage is one of the most important properties for the dimensional stability of wood. Excessive shrinkage during drying causes warping (bowing, cupping, twisting and springing), cracking and angular deformation of wood (Ormarsson *et al.*, 1998; Skaar, 1988). In addition, processed wood expands or shrinks in service according to ambient moisture levels, hence excessive shrinkage can cause unacceptable defects in products, such as flooring and furniture. Therefore, wood with low shrinkage characteristics is highly desirable for sawn-timber production and solid-wood products (Walker, 2006).

Another important factor to consider is that wood is an anisotropic material, i.e. its properties, including shrinkage rates, differs in three directions: tangentially, radially and longitudinally. In general, wood shrinks about twice as much tangentially as radially, and by a very small amount longitudinally (Zobel & Van Buijtenen, 1989; Cave, 1972). Juvenile wood tends to shrink less transversely (radially and tangentially) than mature wood, because it has lower density (Bowyer *et al.*, 2003). A high coefficient of anisotropy (the ratio between tangential and radial shrinkage) causes cupping, cracking and angular deformation in wood during desorption (Chauhan & Aggarwal, 2004; Skaar, 1988). Longitudinal shrinkage, and variations in this parameter over cross-sections of studs, can cause unacceptable springing and/or bowing (Johansson, 2002).

Mechanical properties

Wood stiffness (modulus of elasticity, MoE) and strength (modulus of rupture, MoR) are important properties for three major applications of sawn timber: furniture-making, flooring and structural timber. In most applications, sawn timber is subject to loads that cause it to bend and deform (Dinwoodie, 2000; Tsoumis, 1991), whereas strength in static bending is defined as natural resistance of a material to failure (Dinwoodie, 2000). For lumber and other solid wood products, wood density is generally an indirect quality trait, since there are usually positive correlations between wood density and desirable mechanical properties (Zhang *et al.*, 2004). However, stiffness and strength are also influenced by the cellulose microfibril angle, the proportion of lignin and the extent of spiral grain (Huang *et al.*, 2003; Aggarwal *et al.*, 2002; Chafe, 1990; Nicholson *et al.*, 1975). Hence, for instance, juvenile wood tends to have lower stiffness than mature wood, because it has higher microfibril angles (Burdon *et al.*, 2004).

1.5 Genetic parameters in *Acacia* and other hardwood species

1.5.1 Genetic parameters in *Acacia* species

Genetic variation in growth traits (height, diameter and volume), stem straightness, branching patterns (branch angle and branch thickness) and wood properties (density, shrinkage, stiffness and strength) has been studied and reported from the early stages of some *Acacia* breeding programs. Variation has mostly been studied at provenance levels, but there have been a few studies on genetic variation at family level.

Growth, stem straightness and branching patterns

Provenance trials conducted in several countries have found substantial genetic variation in growth and stem straightness and branching patterns, with important differences between material originating from the three native regions (PNG, Qld and NT), as well as between provenances from the same regions (Nghia, 2003; Luangviriyasaeng & Pinyopusarerk, 2002; Kamis *et al.*, 1994b; Nor Aini *et al.*, 1994). Provenances from Qld and PNG have generally out-performed most of the provenances from NT (Otsamo *et al.*, 1996). In the south of Vietnam, the best-performing provenances have been Wenlock R. (Qld), Halroyed (Qld) and Morehead (PNG), while in the north the best provenances have been Mibini (PNG), Coen River (Qld), Kings Plains (Qld), and Manton (NT). The Dong Nai local race has displayed intermediate to slow growth. *Acacia auriculiformis* also generally grows better and straighter in the south than in the north of Vietnam, showing that differences in climatic and soil conditions affect the growth and development of the species (Kha, 2003; Nghia, 2003).

Studies, particularly in other Acacia species, indicate that the degree of genetic control of growth traits, stem straightness and branching patterns within acacias is low to moderate (Table 2). Reports on coefficients of additive genetic variation (CV_A) for *A. auriculiformis* are scarce. However, for 6-year-old *A. nilotica*, Ginwal & Mandal (2004) found CV_A values of around 7.0% for growth traits.

Generally, positive genetic correlations have been found between growth traits and stem quality traits (stem straightness and forking propensity) in *Acacia* species, such as *A. crassicarpa*, *A. mangium* and *A. nilotica*. For these species, the correlation between growth and stem straightness is reportedly low (Arnold & Cuevas, 2003), but the correlation between growth and forking propensity (axis persistence) is high (Ginwal & Mandal, 2004).

Wood properties

Wood density is by far the most intensively studied wood property. In *A. auriculiformis*, wood density varies both within and between provenances. Significant differences in basic density between *A. auriculiformis* provenances have been reported by Khasa *et al.* (1995) and Mahat (1999), but not between material from the three geographic regions, PNG, Qld and NT (Mahat, 1999). Radial density variation generally increases with age, and large between-tree variation has been observed in this trait in *A. melanoxylon*

(Clark, 2001), *A. mangium* × *A. auriculiformis* hybrids (Kim *et al.*, 2008), and *A. mangium* (Ani & Lim, 1993). Nevertheless, Lim & Gan (2000) reported that for 14-year-old *A. mangium* the density increased from the pith to the intermediate region, then decreased toward the bark, while in the same species the density tends to decrease with increasing height (Lim & Gan, 2000; Ani & Lim, 1993).

Table 2. Published estimates of heritability for growth traits, stem straightness and branching patterns of acacias

Species	Heritability	N° of families	Age (years)	Reference
Height				
A. auriculiformis	0.14	106	3	Luangviriyasaeng & Pinyopusarerk, 2002
	0.33	129	3	Suanto *et al.*, 2008
A. mangium	0.28	120	2.5	Nirsatmanto & Kurinobu, 2002
A. mearnsii	0.04-0.36	26-84	1	Dunlop *et al.*, 2005
A. nilotica	0.21	200	6	Ginwal & Mandal, 2004
Diameter				
A. auriculiformis	0.11	106	3	Luangviriyasaeng & Pinyopusarerk, 2002
	0.40	129	3	Suanto *et al.*, 2008
A. crassicarpa	0.15	164	3	Arnold & Cuevas, 2003
A. mangium	0.08	150	3	Arnold & Cuevas, 2003
	0.26	120	2.5	Nirsatmanto & Kurinobu, 2002
A. nilotica	0.26	200	6	Ginwal & Mandal, 2004
	0.26	200	6	Ginwal & Mandal, 2004
Stem straightness and branching patterns				
A. auriculiformis	0.20	106	3	Luangviriyasaeng & Pinyopusarerk, 2002
	0.24	129	3	Suanto *et al.*, 2008
A. crassicarpa	0.25	164	3	Arnold & Cuevas, 2003
A. mangium	0.10	150	3	Arnold & Cuevas, 2003

For wood stiffness, significant differences between provenances (Nor Aini *et al.*, 1997; Hazani, 1994), between trees and within trees at different heights have also been observed in *A. auriculiformis* (Aggarwal *et al.*, 2002; Kumar *et al.*, 1987; Chomchran *et al.*, 1986; Keating & Bolza, 1982).

The genetic parameters of the species' wood properties have been examined in very few studies. The narrow-sense heritability of wood density in *A. auriculiformis* has been examined in one previous study, and found to be low (0.18) in 3-year-old plants (Suanto *et al.*, 2008). In addition, Nor Aini *et al.* (1997) have examined *A. crassicarpa*, and found broad-sense heritability to be high for wood shrinkage (0.38-0.44) and low for the mechanical properties (0.11-0.12).

Growth traits have been shown to have non-significant negative correlations with wood density (Suanto *et al.*, 2008; Mahat, 1999; Khasa *et* *al.*, 1995) and shrinkage in *A. auriculiformis* (Kumar *et al.*, 1987). In other *Acacia* species like *A. mangium* and in the acacia hybrid (*A. mangium x A. auriculiformis*), Kim *et al.* (2008) and Khasa *et al.* (1995) found non-significant positive correlations between wood density and growth traits.

1.5.2 Genetic parameters in other hardwood species

Growth, stem straightness and branching patterns

The narrow-sense heritability estimates for growth traits are generally low to moderate for most forest tree species (Cornelius, 1994; Eldridge *et al.*, 1993). The heritability estimates for growth traits in tropical hardwood species are usually in the range from 0.1 to 0.3 (Table 3). The value of CV_A generally tends to be below 15% for growth traits, except tree volume, which shows higher levels of CV_A than other traits (Cornelius, 1994).

Table 3. *Published estimates of heritability for growth traits of tropical hardwood species*

Species	Heritability		No of families	Age (years)	Reference
	Diameter	Height			
B. quinata	0.27	0.24	155	8	Hodge *et al.*, 2002
C. spruceanum	0.24	0.31	200	3	Sotelo Montes *et al.*, 2006
G. crinita	0.03	0.08	200	1	Rochon *et al.*, 2007
E. camaldulens	0.14	0.1	114	5	Mahmood *et al.*, 2003
E. grandis	0.14	0.21	47	4.5	Floyd *et al.*, 2003
E. grandis	0.15	0.16	30	5	Gapare, 2003
E. urophylla	0.13		208	3	Arnold & Cuevas, 2003
	0.23	0.24	200	3	Wei & Borralho, 1998
E.grandis	0.16		203	3/5/15	Marco & White, 2002
E.pellita	0.10-0.27	0.22-0.27	60	3	Leksono *et al.*, 2008
	0.42	0.29	171	7.5	Hardiyanto, 2003
E. tereticornis	0.11-0.29	0.05-0.18	91	1.75	Ginwal *et al.*, 2004
T. grandis	0.37	0.28	61	3.5	Callister & Collins, 2008

Note: B=Betula; C=Calycophyllum; G=Guazuma; E= Eucalyptus; T=Tectona

Low to moderate heritability estimates have been reported for branching patterns (branch angle and branch thickness) in *E. nitens* (Whiteman *et al.*, 1992) and *E. globulus* (Volker *et al.*, 1990). Low heritability has also been found for stem straightness in tropical eucalypt species (Leksono *et al.*, 2008; Arnold & Cuevas, 2003; Mahmood *et al.*, 2003; Marco & White, 2002) and other tropical hardwood species, for example *Bombacopsis quinata* (Hodge *et al.*, 2002) and *Tectona grandis* (Callister & Collins, 2008).

Age-age correlations, i.e. the degree of similarity of traits between trees of different ages, have been examined for height and diameter in young trees of several *Eucalyptus* and *Populus* species. The genetic correlations for both height and diameter (at ages over 2 years) are consistently positive and usually high, ranging from 0.87 to 1.0 in *Eucalyptus* species (Osorio *et al.*, 2003; Wei & Borralho, 1998; Greaves *et al.*, 1997; Raymond *et al.*, 1997; Borralho *et al.*, 1992a; Borralho *et al.*, 1992b). In *Populus deltoides*, Kumar & Singh (2001) also found high age-age correlations between age of 6 years and younger (2-5 years) ages for growth traits. The high genetic age-age correlations for growth traits generally suggest there are good prospects for selecting trees that will grow rapidly at young ages.

Inter-trait correlations between growth traits and desirable stem quality traits, such as stem straightness, branch number and branch angle, have also been found to be positive and significant for *E. grandis* and *E. camaldulensis* (Gapare, 2003; Mahmood *et al.*, 2003).

Wood basic density

Results from several reviews of a large number of tree species indicate that the CV_A for the basic density of diverse hardwood species is ca. 5% (Hamilton & Potts, 2008; Stener & Hedenberg, 2003; Cornelius, 1994), whereas the values for height and diameter are ca. 8.1 and 8.6%, respectively (Cornelius, 1994). In contrast, the heritabilities for height and diameter are reportedly lower (ca. 0.2) than for wood density (> 0.3, similar to published values for many hardwood species; see Table 4).

Table 4. Published estimates of heritability (h^2) for basic wood density of various commercial hardwood species.

Species	Heritability	No of families	Type	Age (years)	Reference
B. pendula	0.73[1]	78	cl	10	Stener & Hedenberg, 2003
C. spruceanum	0.53-0.65	200	op	3	Sotelo Montes *et al.*, 2006
E. camaldulensis	0.67[1]	78	cl	3	Varghies *et al.*, 2008
E. dunnii	0.42	50	op	6.5	Arnold *et al.*, 2004
E. globulus	0.65	65	op	8	Borralho *et al.*, 1993
	0.41[a]	411	op	5	MacDonald *et al.*, 1997
	0.87	39	op	8	Muneri & Raymond, 2000
E. grandis	0.34	41	op	8	Santos *et al.*, 2004
	0.35[1]	65	cl	6	Osorio *et al.*, 2001
E. nitens	0.72	50	op	7	Greaves *et al.*, 1996
	0.60[a]	50	op	7	Greaves *et al.*, 1996
E. urophylla	0.64[a]	51	op		Wei & Borralho, 1997
	0.71	51	op		Wei & Borralho, 1997
P. occidentalis	0.73	31	op	7-8	Nebgen & Lowe, 1982
Q. petraea	0.56[1]	30	cl	22	Nepveu, 1984
Q. robur	0.59[1]	22	cl	22	Nepveu, 1984
Q. rubra	0.37[1]	16	cl	22	Nepveu, 1984

Note: op= open pollinated; cl = clones; [a]= heritability estimates based on Pilodyn penetration; [1]=repeatability; B=Betula; C=Calycophyllum; E= Eucalyptus; P=Platanis; Q=Quercus

Previously published age-age correlation estimates for the wood density of hardwood species are restricted to those obtained in a study of *E. nitens*, in Australia, in which very high correlations between annual ring densities from year 3 onwards were found (r_A>0.80; (Greaves *et al.*, 1997)).

Wood density and growth traits generally have negative genetic correlations, and the genetic correlation between wood density and diameter is generally more strongly negative than the correlation between density and height. However, the strength of these correlations varies between species. Raymond (2002) reviewed published estimates for genetic correlations between wood density and growth in eucalypt species, which were variable but often close to zero, and concluded that there was no convincing evidence for a strong negative relationship between growth and density in those species.

Wood shrinkage and mechanical properties

There is little published information on the shrinkage and mechanical properties of hardwoods, largely because of the high costs of sawing studies and the lack of genetic trials with mature material to test. However, previous results have shown wood shrinkage properties to be moderately to highly inherited (Table 5), with CV_A values of around 8% (Hamilton *et al.*, 2009; Bandara, 2006; Koubaa *et al.*, 1998). For mechanical properties, significant genetic variation has also been reported for juvenile wood of hybrid poplar clones (Hernandez *et al.*, 1998), families of *E. grandis* (Santos *et al.*, 2004), and provenances of *T. grandis* (Bhat & Priya, 2004). Published heritability estimates for mechanical properties are also moderate to high in hardwood species (Table 5) and the CV_A values for these properties is reportedly around 4.0% (Santos *et al.*, 2004).

The relationships between tree growth and wood shrinkage parameters vary depending on the species studied and, presumably, the relationship between growth and wood density for each species. For instance, the correlation between tree growth and wood shrinkage is reportedly negative for eucalypt species (Hamilton & Potts, 2008; Bandara, 2006; Chafe, 1994) and *Terminalia superba* (Hock & Mariaux, 1984), but positive for *Quercus* species, *C. spruceanum* (Sotelo Montes *et al.*, 2007b; Nepveu, 1984) and *Gilbertio dendron dewevrei* (Hock & Mariaux, 1984). The correlation between these traits has been found to be insignificant for *T. grandis* (Hock & Mariaux, 1984) and *P. deltoides x P. nigra* hybrid clones (Koubaa *et al.*, 1998). Shrinkage has been found to depend on wood density, fibre-saturation point (FSP), wood chemical composition and microfibril angle (MFA) (Walker, 2006; Sekhar *et al.*, 1967). Wood density also appears to affect shrinkage parameters more than FSP (Sekhar *et al.*, 1967).

Table 5. *Published estimates of heritability (h^2) for wood shrinkage, stiffness and strength of commercial hardwood species.*

Species	Heritability	No of families	Type	Age (years)	Reference
Shrinkage					
C. spruceanum	0.21-0.50	200	op	3.3	Sotelo Montes *et al.*, 2006
E. grandis	0.29-0.44	50	op	4.5	Bandara, 2006
E. nitens	0.38	400	op	9	Hamilton *et al.*, 2009
	0.23-0.61[a]				Hamilton & Potts, 2008
P. deltoides x P. nigra	0.13-0.33[1]	10	cl	9	Koubaa *et al.*, 1998
Stiffness					
E. grandis	0.57	41	op	8	Santos *et al.*, 2004
E. dunnii	0.26	47	op	9	Henson *et al.*, 2004
C. spruceanum	0.47	200	op	3.3	Sotelo Montes *et al.*, 2007a
P. deltoides x P. nigra	0.34[1]	10	cl	9	Hernandez *et al.*, 1998
Strength					
E. dunnii	0.57	47	op	9	Henson *et al.*, 2004
P. deltoides x P. nigra	0.47[1]	10	cl	9	Hernandez *et al.*, 1998

Note: op= open pollinated; cl = clones; [a]=heritabilities from a review of 100 field tests; [1]=repeatability; C=Calycophyllum; E= Eucalyptus; P=Populus

In a study of 16 softwood and hardwood species, Zhang (1995) found that the relationship between mechanical properties and growth rate could be either positive or negative, depending on the species. However, the growth rate appears to have markedly less effect on the wood of hardwood species (in terms of mechanical properties) than that of softwood species. Furthermore, in hardwood species wood stiffness seems to be markedly less influenced by the growth rate than wood strength, mechanical properties are generally more influenced by growth rate than wood density, and the relationships between mechanical properties and wood basic density are positive (Innes, 2007; Yang & Evans, 2003; Evans & Ilic, 2001; Zhang, 1995). In eucalypts, MFA alone accounted for 87 % of the variation in stiffness, density alone accounted for 81 %, and the density/MFA ratio accounted for 92 % of the variation in the wood stiffness (Yang & Evans, 2003).

1.5.3 Genotype-environment interactions affecting growth and wood properties in acacias and other hardwood species

For growth traits (diameter and height), significant G×E interactions have been reported in *A. auriculiformis, A. mangium* and *A. mearnsii* (Dunlop *et al.*, 2005; Khasa & Bousquet, 2001; Kamis *et al.*, 1994a), and in various eucalypts (Matheson & Raymond, 1996), including *E. tereticornis* (Otegbeye, 1991), *E. camaldulensis* (Otegbeye & Samarawtra, 1992), *E. globulus* (Costa E Silva *et al.*, 2006; Raymond *et al.*, 2001), and *E. urophylla* (Wei & Borralho, 1998). Similarly, G×E interactions have been found to be significant, but weak, for density and cellulose content of *E. nitens* (Kube *et al.*, 2001). However, they are reportedly unimportant for density and bark thickness in *E. urophylla* (Wei & Borralho, 1997), density in *E. grandis* (Osorio *et al.*, 2001) and fibre length in *E. nitens* (Kube *et al.*, 2001). In a study of *E. globulus* at three sites, Raymond *et al.* (2001) also found that G×E interactions did not have major effects on a pulp production index (combining tree diameter, basic density and predicted pulp yield data into a single variable) of *E. globulus*.

To summarise, these findings indicate that G×E interaction may be of importance for growth traits, but of less importance for wood density. For wood mechanical properties of hardwood species there is no available information concerning G×E interactions.

2 Aims

The overall aim of the work underlying this thesis was to increase knowledge of genetic variation in economically important traits for sawn timber products of *A. auriculiformis* in Vietnam. The results should provide tree breeders with relevant information to establish and refine breeding and deployment programs of the species. The following specific questions were addressed:

1. How strong is the genetic variation and degree of genetic control for growth, stem straightness (I), wood basic density (II), wood shrinkage (III), wood stiffness and wood strength (IV)?
2. How is selection for growth traits likely to affect wood properties in juvenile wood and mature wood (II, III, and IV)?
3. How strong are the relationships between juvenile and mature wood for the studied traits and what is the most efficient selection age for these traits (I, II, III and IV)?
4. How strong are the genotype by environment interactions for growth and stem straightness (I and V)?
5. How large are the predicted and realised gains from the breeding of *A. auriculiformis* (V)?

3 Materials and methods

The materials examined in the studies underlying this thesis were plants in a progeny test, three clonal tests and three genetic gain tests, located in northern, central and southern Vietnam (Figure 2). In the north, mean annual temperature is 23°C, with limitation of low temperature in the winter months. The soil was a yellow ferralitic clay loam with strong laterisation evident in the profile, acidic (pH 3.5–4.5), and infertile, with low levels of phosphorus and potassium. Climatic and soil conditions in the centre are similar in the north, and less favourable for growth of *A. auriculiformis* than in the south, where the soil is deep, with a light texture, and the amplitude of mean temperature is from 24 to 30^{0}C (Kha, 2003).

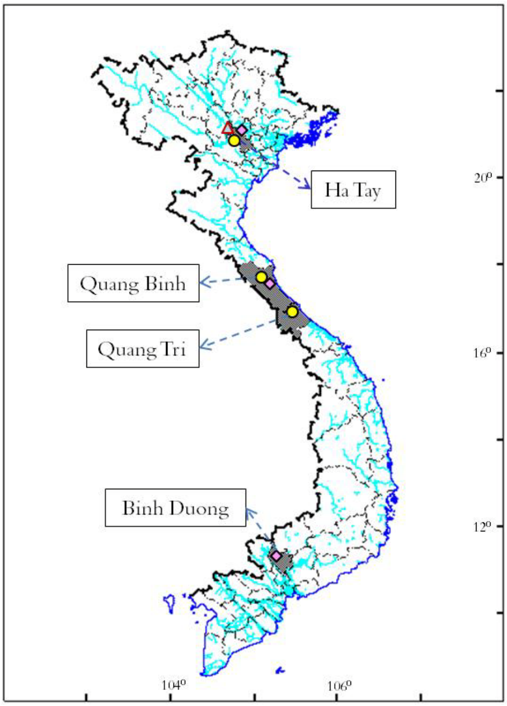

Figure 2. Locations of studied genetic trials in Vietnam (*△ progeny test; ◇ clonal test; ○ genetic gain test)*

Information about the traits studied and the genetic materials in the tests is summarized in Table 6. The genetic gain tests are comparing seedlots representing various levels of genetic improvement, and appropriate controls, generated from five or six of the following materials: (1) an SSO (seedling seed orchard) select trees seedlot, (2) an SSO routine seedlot, (3) an SPA (seed production area) select trees seedlot, (4) a mix of seed from the best natural provenances, (5) a commercial control seedlot and (6) a mix of four superior clones.

Table 6. *Number of clones/families and traits studied in each test and paper*

Test	No of clones/ families/treatments	Age (years)	Traits studied	Paper
Progeny test				
Ha Tay	140 families	9	Diameter, height, stem straightness, forking, knot index, bark thickness, wood density, and Pilodyn penetration	II
Clonal test				
Ha Tay	102 clones	3	Diameter, height, stem straightness and branch thickness	I
Quang Binh	114 clones	3	Diameter, height, stem straightness and branch thickness	I
Binh Duong	120 clones	4	Diameter, height, stem straightness and branch thickness	I
	40 clones	5.5	Shrinkage	III
	40 clones	5.5	Bending stiffness and strength	IV
Genetic gain test				
Ha Tay	5 treatments	4	Diameter, height, stem straightness, and forking	V
Quang Binh	6 treatments	4	Diameter, height, stem straightness, and forking	V
Quang Tri	5 treatments	4	Diameter, height, stem straightness, and forking	V

Growth traits and stem straightness of all trees in the tests were recorded annually. The stem straightness, forking and branch thickness were scored using a scale with 5-6 classes. Knot indices were calculated from data on branch numbers and ratio of diameter of the largest branch to stem diameter (Doede & Adams, 1998). Bark thickness was measured using a bark gauge.

Wood density was measured indirectly using Pilodyn pin penetration, and directly on increment cores using the water displacement method (Olesen, 1971). The studies of shrinkage and mechanical traits, modulus of elasticity (MoE) and modulus of rupture (MoR), were based on measurements on small clear-wood specimens. The measurements and the sizes of the test samples are indicated in Figure 3.

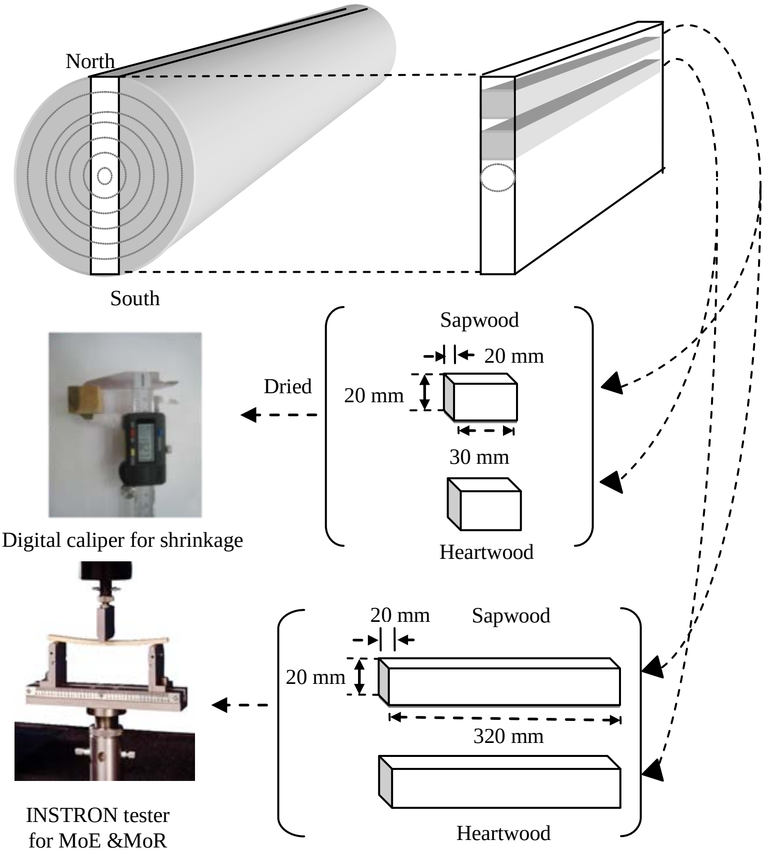

Figure 3. Sampling strategy for studies of wood properties and dimensions of the samples.

The statistical analyses were conducted in two steps: (i) univariate analysis, where variance components for each trait were estimated and (ii) bivariate analysis to estimate variances and covariances between pairs of characters. Mixed linear models were used in both steps. REML estimates of the (co)variance components were obtained using ASReml software (Gilmour *et al.*, 2006). Genetic parameters, such as heritability, coefficients of variation and genetic correlations were based on the estimated variances and covariances.

4 Main results and discussion

4.1 Genetic parameters for important traits

The coefficients of variation and heritability estimates of some of the studied traits are presented in Table 7 and 8. The results show that there is substantial genetic variation and degree of genetic control for growth traits, stem straightness, wood density, total shrinkage, static bending stiffness and strength. The estimated gains from single-trait selection indicate that considerable genetic improvement of *A. auriculiformis* can be achieved for sawn timber production from both the open-pollinated population and the populations of clones examined.

Table 7. *Coefficients of additive genetic variation (CV_A), heritability (h^2) and gain estimates from selection of the best individuals within the best families for growth traits, stem straightness, and wood density at 9 years of age*

Trait	Description	CV_A	h^2	Gain (%)[1]
DBH	Diameter at breast height	7.0	0.36±0.10	12.4
HT	Height	11.2	0.36±0.09	19.8
STR	Stem straightness	0.49[2]	0.27±0.10	1.56[3]
DEN	Basic density	9.0	0.55±0.12	18.5

Note: [1] *Estimated gain from single-trait selection based on selection proportion of 30% (i=1.14) for families and the best individual of 8 within the best families (i=1.424).* [2] *Additive standard deviation of real stem straightness expressed in a scale with 5 classes.* [3] *The gain expressed in additive standard deviation. The coefficient of relationship was assumed to be 0.33 when calculating within-provenance heritabilities (h^2).*

At nine years of age, estimated coefficients of additive genetic variation (CV_A) ranged from 7% to 11% for growth traits (Table 7). The CV_A value for density was around 8% at different ages (Table 3, Paper II). Individual tree heritability estimates for both growth and stem straightness were moderate (0.27-0.36). Wood density had higher individual tree heritability (0.55) than the growth traits (Table 7). This finding is consistent with data compiled by Cornelius (1994) for a large number of tree species. The values of CV_A, heritability and predicted genetic gain in the tests considered in this thesis may have been affected by two within-family selective thinnings carried out at age of 3 and 5 years (in which up to three trees from each original four-tree family plot were removed, but all families were retained in the trial). This may have reduced the error variance and given a bias in heritability as well as gain calculations. Heritabilities for height and diameter at breast height at age 9 years were substantially higher than those at ages of 3 and 5 years, prior to the first and second thinnings, respectively.

Table 8. *Coefficients of genotypic variation (CV_G), clonal repeatability (H^2) and gain estimates from clonal deployment for growth traits, stem straightness, wood density, wood total transverse shrinkage, stiffness and strength at age of 5.5 years*

Trait	Description	CV_G	H^2	Gain (%)[(1)]
DBH	Diameter at breast height	6.7	0.29±0.08	9.7
HT	Height	3.4	0.20±0.07	4.5
STR	Stem straightness	0.41[(2)]	0.28±0.08	0.6[(3)]
DEN	Basic density	4.7	0.47±0.08	7.5
T	Total tangential shrinkage	7.6	0.32±0.08	11.2
R	Total radial shrinkage	7.5	0.38±0.08	11.5
MoE	Static bending stiffness	11.1	0.57±0.07	13.6
MoR	Static bending strength	6.3	0.29±0.08	9.2

Note: [(1)]-Estimated gain from single-trait selection. [(2)]Genotypic standard deviation of real stem straightness expressed in a scale with 5 classes. [(3)] The gain expressed in genotypic standard deviation. A selection proportion of 10% was used in the calculation

At age 5.5 years, the values of coefficients of genotypic variation (CV_G) for growth traits and wood density were low (Table 8). The CV_G values for shrinkage, stiffness and strength were higher than those of growth traits. Moderate estimates of clonal repeatability at age 5.5 years (0.20-0.38) were found for growth, stem straightness, total transverse shrinkage traits and static bending strength. However, repeatability estimates for static bending stiffness were high (0.57).

The individual tree heritability and clonal repeatability estimates for growth traits, stem straightness, density and shrinkage increased with age (I, II, III and IV). There was no consistent pattern of differences for the estimates of H^2 for mechanical properties between heartwood (HW) and sapwood (SW), implying that the genetic control of wood mechanical properties is stable with age.

The predicted gains, based on the gathered data, were high for growth and wood properties (Table 7 and 8). The gains for the best individual within the best families in forward selection for breeding were 19.8 and 12.4% for HT and DBH, respectively, and 18.5% for DEN (Table 7). The gain in stem straightness was expressed as improvement of 1.56 classes in a scale with 5 classes. The gains from selection of the best clones ranged from 9.2-13.6% for shrinkage and mechanical properties (Table 8).

4.2 Age-age correlations and relative selection efficiency

Strong age-age genotypic correlations were observed for growth traits, wood density, total transverse shrinkage, stiffness and strength between heartwood and sapwood (Table 9), indicating that heartwood (younger) traits are good genetic indicators of the sapwood (older) traits. Therefore, there will be more gain per unit time with selection at an earlier age.

Table 9. *Age-age additive genetic correlation (r_A), age-age genotypic correlation (r_G) for height, diameter, total transverse shrinkage and mechanical traits (for meanings of abbreviations see Tables 7 and 8*; ages in parentheses*)*

Trait (age)	r_A	r_G
HT(3) vs HT(9)	0.64±0.17	
HT(5) vs HT(9)	0.91±0.08	
DBH(3) vs DBH(9)	0.86±0.10	
DBH(5) vs DBH(9)	0.93±0.05	
STR(5) vs STR(9)	0.87±0.18	
VOL(5) vs VOL(9)	0.91±0.05	
DEN(3) vs DEN(9)	1.02±0.03	
DEN(6) vs DEN(9)	0.99±0.02	
T_{hw} vs T_{sw}		0.87±0.20
R_{hw} vs R_{sw}		0.95±0.26
MoE_{hw} vs MoE_{sw}		0.99±0.05
MoR_{hw} vs MoR_{sw}		0.88±0.18

Note: Ages of the density traits are approximated; $_{hw}$ heartwood trait; $_{sw}$ sapwood trait

Juvenile-mature and age-age correlations are important for evaluating the possibility of early selection and determining the best selection age (Falconer & Mackay, 1996). Analyses of results of forward selection for the growth traits and wood density in the *A. auriculiformis* provenance-progeny trial we examined showed that higher genetic gains per unit time would be achieved with selection at ages of 3 or 5 years, than at 9 years (Table 5, Paper II), and overall the results indicate that the optimum age for selection could be as low as three years for growth traits and wood density in *A. auriculiformis* breeding programs. Similarly, Raymond (2002) reported that early selection for wood basic density could be applied at age 3 years in *Eucalyptus* species, which display high heritability. It should be relatively easy to select for growth, stem straightness and wood density at this age. However, material with desirable forking, knot index, and other wood properties cannot be selected for effectively at 3 years of age in northern Vietnam, because the trees will still be too small (mean height ca. 7 m and mean DBH ca. 7 cm; II). Five years is probably the minimum age for the expression of these traits in the north (DBH ca. 11 cm at 5 years).

4.3 Genetic correlations and correlated responses to selection for diameter and density

Diameter and height showed consistent, positive genetic and genotypic correlations with stem straightness, but non-significant negative correlations with wood properties, except for a negative correlation between diameter and stiffness (Table 10). These findings show that selection for growth traits would positively affect stem straightness and negatively affect wood stiffness, but have only minor effects on wood density and shrinkage.

Table 10. Genotypic correlations between growth and quality traits, and correlated responses to direct selection at 10% selected for diameter and density. For meanings of abbreviations, see Tables 7 and 8.

	HT	DBH	DEN	Response to indicated traits when selecting for	
				DBH	DEN
MoE	-0.26±0.25	-0.25± 0.23	**0.62**±0.14	-4.1	10.3
MoR	-0.13±0.36	**-0.56**±0.16	0.27±0.18	-8.2	4.5
R	-0.01±0.25	-0.14±0.22	0.22±0.20	-2.5	4.4
T	-0.04±0.26	-0.12±0.23	0.25±0.20	-2.3	5.2
DEN	-0.07±0.18 [a]	-0.08±0.19 [a]		-3.5	
STR	**0.79**±0.15[a]	**0.96**±0.13[a]		4.7	

Note: [a] Genetic correlation; significant ($p<0.05$) correlations in bold

Both shrinkage and mechanical properties showed positive correlations with wood basic density (Table 10). However, as for the correlations with growth traits, not all of the correlations between wood density and wood properties were significantly different from zero (Table 10). Nevertheless, the estimated genetic correlations between wood strength and density are positive and moderate for both the heartwood and sapwood. Therefore, early selection based solely on density could result in improvements in both heartwood and sapwood strength.

Predictions of genetic responses indicated that selection for diameter would have minor impact on wood density. Selection of the 10% best clones for diameter would decrease the wood density at age 9 years by 3.5%, or 20 kg/m^3, and increase the stem straightness score by 4.7%. The tangential and radial shrinkage, strength and stiffness parameters showed weak negative responses to selection for clone diameter, with declines of 2.3%, 2.5%, 4.1 % and 8.2%, respectively, from direct selection for this trait (Table 10). Improvement of density (by 10%) would increase stiffness by 4% and strength by 10.3%. However, this improvement would decrease the dimensional stability of *A. auriculiformis*, with an increase of approximate 4-5% in total transverse shrinkage.

Since the genetic correlation between Pilodyn penetration and wood basic density was strong and negative, lower density resulting in higher penetration (r_A=-0.88), Pilodyn penetration is generally reliable as an indirect measure of wood basic density in *A. auriculiformis*. In addition, the strong positive associations between total and partial shrinkage traits (Table 6, Paper IV) indicated that total shrinkage, which is easily measured, could be the best character for assessing wood shrinkage traits.

4.4 Genotype by environment interactions affecting growth and stem straightness

The genetic correlations for growth and stem straightness between test sites were all significantly different from one, but the correlations between pairs of test sites did not differ significantly from one another. Many clones contributed to the interactions. The correlations ranged from low to moderate (0.06 to 0.52) for most traits (Table 11), except for the correlation of STR between Quang Binh and Binh Duong (0.79). The low between-sites genotypic correlations observed in this study could be explained by between-site differences in both soil and climatic conditions (Kha, 2003). Clone-by-site interactions were found to be strongest in comparisons of Ha Tay (northern Vietnam) and Binh Duong (southern Vietnam) clone trials and weaker in comparisons of the trials located at Quang Binh (central-north Vietnam) and Ha Tay, which have more similar environments (Table 11). Therefore, G×E effects are clearly of practical importance for clonal development and different clones should be used in different regions.

In contrast, the rankings of seedlots for height, diameter, stem straightness, forking and volume in a realised gain test series across the three trial sites (Ha Tay, Quang Binh and Quang Tri) were relatively stable. This indicates that seedlot-by-environment interaction is of little practical significance (Paper V). The rankings of the seedlots across three genetic gain tests could be influenced by genetic buffering. Each seedlot in the tests consisted of mixed seeds from many parents, with different genotypes. Within a seedlot, different genotypes may prosper at different sites, providing greater stability of performance at the stand level than is obtained by use of an individual clone.

Table 11. *Genotypic correlations between sites for growth traits and stem straightness at 3 years of age (for meanings of abbreviations see Table 7)*

Trait	Site	Quang Binh	Binh Duong
HT	Ha Tay	0.30 ±0.14	0.42±0.13
	Quang Binh		0.52±0.12
DBH	Ha Tay	0.50±0.15	0.06±0.14
	Quang Binh		0.35±0.14
VOL	Ha Tay	0.44±0.16	0.45±0.12
	Quang Binh		0.43±0.14
STR	Ha Tay	0.37±0.15	0.41±0.13
	Quang Binh		0.79±0.09

4.5 Genetic gains from the present breeding program in Vietnam

Estimates of genetic gain from the present breeding program in Vietnam (V) indicated that there is strong potential for gains in growth, both within and between seed sources. The SSO select trees seedlot provided the best performing plants at all three sites (Ha Tay, Quang Binh and Quang Tri), followed by the SPA select trees seedlot and SSO routine seedlots, then the mixture of seed from the best natural provenances, while the commercial seedlot yielded the most slowly-growing plants at all three sites. The across-site estimates of realised gain for DBH, expressed as the percentage gain relative to the DBH of trees originating from the mixture of seed from the best natural provenances, were 16% for the SSO select trees seedlot, 7% for the SPA select trees seedlot and 7% for the SSO routine seedlot. Plants originating from the SSO and SPA seedlots had significantly straighter stems and lower frequencies of stem forking than those originating from the mixture of seed from the best natural provenances, which were in turn superior to plants originating from the commercial seedlot.

5 Implications for tree improvement of *A. auriculiformis* in Vietnam

5.1 Improvement of wood properties

Acacia auriculiformis has sufficiently high wood stiffness (MoE=17.2-24.2 GPa) and strength (MoR=128-168 MPa) for the Vietnamese furniture industry. Hence there is now no strong requirement to increase the wood's mechanical properties. However, wood quality (density, dimensional stability, strength and freedom from defects) may become important objectives in advanced breeding programs of *A. auriculiformis* in the future. Improvement of basic density and total transverse shrinkage (T and R) may be more important than improvement of other properties for *A. auriculiformis* wood (II, III). Reduction of shrinkage anisotropy (the ratio between T and R) will become more important when the use of drying technology becomes more popular and commonly adopted (Walker, 2006) in Vietnam.

In the first one or two generations, the improvement program has to focus on increasing stem volume (especially diameter) and improving stem quality (increasing stem straightness and reducing forking), in order to improve the recovery of solid wood products and reduce harvesting costs for pulpwood. Improving volume is very important if *A. auriculiformis* is to compete with faster-growing alternatives like the widely planted acacia hybrid clones. Otherwise, the area of *A. auriculiformis* plantations will continue to shrink, even though it provides higher quality wood than the hybrid. The high realised and predicted genetic gains for growth traits (10.1 -12.4% for diameter) show the potential of improvement in tree volume from the breeding program (Table 7 and Paper V).

Since the number of families in the present base population is limited (203 unrelated families), new genetic material has to be included in the breeding program to establish new long-term populations. In addition, to increase future management options (including exploitation of favourable G×E interactions), it has been suggested by Namkoong (1981) for the Vietnamese program that separate populations should be formed for long-term breeding to optimize specific traits, such as stem volume and/or wood properties.

A selection index based on genetic parameters and economic weights dependent on the specific breeding objectives (Raymond, 2002; Borralho *et al.*, 1993) could deliver significant benefits in breeding. For example, an index based on diameter, basic density and total transverse shrinkage of heartwood, combined with a threshold value for stem straightness and forking, could improve growth, stem quality, basic density and shrinkage. Moreover, inclusion of density and shrinkage, assessed at an early age, in a selection index would improve both heartwood and sapwood shrinkage, because of the high juvenile-mature genetic correlations for these traits. The weightings of the two terms could depend strongly on the relative importance attached to improving shrinkage in the heartwood and sapwood, respectively. Bio-economic modelling of *Acacia* growing and processing systems in Vietnam is needed, to identify the most important breeding objectives and to determine relative weights of the appropriate traits, as has been done for *Pinus radiata* in Australia (Ivkovic *et al.*, 2006).

Another option is that the industry could use large volumes of wood from clones of the *A. mangium* x *A. auriculiformis* hybrid, which is less dense and weaker than *A. auriculiformis* wood (Kim *et al.*, 2008; Kha, 2001), and stems of the hybrid break relatively easily during strong wind (Mai, 2009). Breeding using elite individuals of both the parent species with improved wood properties would be useful in order to breed new hybrid clones with increased stiffness and strength.

5.2 Clonal deployment

Clonal forestry using selected individuals of *A. auriculiformis* mass-propagated from stem cuttings (I) will capture favourable non-additive genetic variation, as well as additive genetic variation that is obtained through sexual breeding (Libby & Rauter, 1984). With *A. auriculiformis*, clonal forestry is often used, allowing the possibility of selecting clones that are "correlation breakers", i.e. individuals in which existing correlations between growth and wood quality traits no longer occur. If correlation breakers can be identified, selection of individuals with outstanding wood quality values would provide a simple, feasible way to improve the uniformity of *A. auriculiformis* wood and thus increase manufacturing efficiency.

In clonal deployment programs, it may be necessary to either limit the number of wood properties in a selection index, or relax threshold values of some of the traits, in order to ensure that the best selections are obtained within the limited resources of the program (Verryn, 2008). In the current study population of 40 *A. auriculiformis* clones, no clone met the test criterion of being within the top 10% for three target traits (diameter, density and shrinkage). When the selection criteria were relaxed to "above-average value of population" thresholds of being in the best 48% of the population (diameter at breast height and density), and 47% (shrinkage), assuming independence of traits, the probability P_C of finding a clone satisfying all these criteria would be $P_C = 0.108$ or 4.33 in 40. Actually, it was found that one clone in the trial met all criteria at these levels of selection. Further to these three traits, there was a need to select for at least another trait (stem straightness). Assuming a 50% threshold for straightness, this equates to probabilistic value of $P_C = 0.108 \times 0.5 = 0.054$, or 5 in 100 clones. Clearly, there needs to be a reduction in the number of traits, or further relaxation of selection criteria, if sufficient clones for deployment are to be obtained from modest clonal programs testing only a few hundred clones.

Significant G×E interaction effects were found in growth and stem quality traits, i.e. the most promising clones were not the same at Ha Tay, Quang Binh and Binh Duong (I). To manage G×E interactions, the best clones could be selected for specific sites to maximize deployment gains. This would involve identifying different plantation regions, representing homogenous environmental zones within which selections are deployed. Separate deployment populations in different zones would also be established.

6 Further research

Cheaper and more rapid methods for measuring shrinkage and mechanical properties than the analyses of wood blocks used in these studies are needed. There are some obvious alternatives, which have been demonstrated to provide data that correlate strongly with direct measurements, and explain 70-98% of the variation derived from direct measurements (Huang *et al.*, 2003; Baillères *et al.*, 2002; Jayawickrama, 2001). For shrinkage, near infrared diffuse reflectance spectroscopy (NIRS) is a highly promising method that could be adapted for rapid measurements on wood (Baillères *et al.*, 2002), and dynamic MoE could be assessed by measuring sonic resonance frequencies of small axial samples of sapwood (Ilic, 2003). In addition, FAKOPP and DIRECTOR-ST300 acoustic tools can be used to assess MoE quickly on standing trees and logs (Huang *et al.*, 2003; Lindstrom *et al.*, 2002). Further studies are needed to determine the most effective tools for indirect measurements of shrinkage and mechanical properties of *A. auriculiformis* wood. Studies of genotype by environment interactions for these wood quality traits are also needed.

Bio-economic modelling (Ivkovic *et al.*, 2006) of *Acacia* growing and processing systems in Vietnam is needed, in order to identify the most important traits for objective improvement at particular rotation ages. There is a need to determine relative weights of these traits and to link them to traits that can be assessed in younger trees for early selections in genetic trials.

One rapidly expanding area of research is genetic mapping. In eucalypt species, major candidate genes and quantitative trait loci (QTL) have been found for traits such as volume growth, stem form, wood specific gravity, fibre length, pulp yield and microfibril angle (Thamarus *et al.*, 2004; Verhaegen *et al.*, 1997; Grattapaglia *et al.*, 1996). Since trees have long generation times, most studies have relied on single pedigrees to determine the number and size of QTLs affecting quantitative trait variation. However, it is important to validate QTLs in additional pedigrees (Kumar *et al.*, 2000), because of the highly heterozygous, outbreeding nature of most tree species. Identification of QTLs affecting wood and fibre properties will lead to a greater understanding of these traits and help in selection and manipulation of these traits in *A. auriculiformis* breeding programs.

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