

Improvement of *Eucalyptus* plantations grown for pulp production

Nguyen Duc Kien

*Faculty of Natural Resources and Agricultural Sciences
Department of Plant Biology and Forest Genetics
Uppsala*

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Cover: Five-year-old clonal plantation of *Eucalyptus camaldulensis* in southern Vietnam (Photo: Nguyen Duc Kien)

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Abstract

The objective of the studies this thesis is based upon was to increase knowledge of the genetics of traits related to wood volume, wood density and pulp yield in *Eucalyptus urophylla* and *E. camaldulensis* that could be used to enhance and accelerate tree improvement programs in Vietnam. Two provenance-progeny trials of *E. urophylla* in northern Vietnam testing 144 families, and three clonal trials of *E. camaldulensis* in southern, north-central and northern Vietnam testing a total of 172 clones were examined in these studies.

In *E. urophylla*, significant between-provenance differences in growth traits were observed, but not in wood basic density or cellulose content. Estimated within-provenance heritabilities were 0.10–0.30 for growth traits, 0.60 for density and 0.50 for cellulose content. Estimated coefficients of additive genetic variation were 10% for growth traits, 6% for density and 4% for cellulose content. Selection efficiency for growth traits was found to be maximal at an age of 2–3 years, with an anticipated rotation period of 5–10 years. Genetic correlations between growth traits and density (0.10–0.28), growth traits and cellulose content (0.28–0.45), and cellulose content and density (–0.02) did not differ significantly from zero. Genetic correlations between the two sites in northern Vietnam, which were 60 km apart and had similar climate and soils, were high for both growth traits and wood density.

In *E. camaldulensis*, clonal repeatabilities at ages 3 and 5 years were 0.18–0.42 for growth traits and 0.71–0.78 for density. The coefficient of genotypic variation was about 13% for growth traits and 6% for density. Genotypic correlations between growth traits and density (–0.16–0.24) did not differ significantly from zero. Between-site genotypic correlations were in the ranges of 0.32–0.56 for growth traits and 0.72–0.88 for density. Selection gains for diameter at breast height at each site at a selection proportion of 5% were 22–32%, with minor effects on density. Selection for diameter based on rankings of material at one site would yield gains in diameter at the other two sites that were only 40–60% of the gains obtainable from direct selection at those sites.

Results from the studies suggest that considerable genetic improvement in eucalypt plantations grown for pulp production in Vietnam can be achieved through breeding and appropriate deployment. Strategies for management of genotype by environment interactions in breeding and clonal deployment of these species are discussed.

Keywords: cellulose content, clonal repeatability, *Eucalyptus camaldulensis*, *E. urophylla*, genetic correlation, genotype by environment interaction, heritability, wood basic density.

Author's address: Nguyen Duc Kien, SLU, Department of Plant Biology and Forest Genetics, P.O. Box 7080, 750 07 Uppsala, Sweden.

E-mail: Nguyen.Duc.Kien@vbsg.slu.se or Nguyen.Duc.Kien@fsiv.org.vn

Dedication

To my family

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List of Publications

This thesis is based on the work described in the following papers, which are referred to by the corresponding Roman numerals in the text:

- I Kien, N.D., Jansson, G., Harwood, C. & Thinh, H.H. (2009). Genetic control of growth and form in *Eucalyptus urophylla* in northern Vietnam. *Journal of Tropical Forest Science* 21(1), 50-65
- II Kien, N.D., Jansson, G., Harwood, C., Almqvist, C. & Thinh, H.H. (2008). Genetic variation in wood basic density and pilodyn penetration and their relationship with growth, stem straightness, and branch size for *Eucalyptus urophylla* in northern Vietnam. *New Zealand Journal of Forestry Science* 38(1), 160-175.
- III Quang, T.H., Kien, N.D., von Arnold, S., Jansson, G., Thinh, H.H. & Clapham, D. (2009). Relationship of wood composition to growth traits of selected open-pollinated families of *Eucalyptus urophylla* from a progeny trial in Vietnam. *Submitted*.
- IV Kien, N.D., Quang, T.H., Jansson, G., Harwood, C., Clapham, D. & von Arnold, S. (2009). Cellulose content as a selection trait in breeding for kraft pulp yield in *Eucalyptus urophylla*. Accepted for publication in *Annals of Forest Science*.
- V Kien, N.D., Jansson, G., Harwood, C. & Almqvist, C. (2009). Clonal variation and genotype by environment interactions in growth and wood density in *Eucalyptus camaldulensis* at three contrasting sites in Vietnam. *Submitted*

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1 Introduction

Concomitant with a 1.5% annual increase in the world's population is a 1.3 to 2% annual increase in global demand for wood products, which translates to a 30–50% increase over the next 20 years (FAO, 1995; McLaren, 1999). This increase in demand is occurring simultaneously with a decrease in the total area of forests in the world and increasing pressure to conserve much larger areas of the world's natural forests for purposes other than wood production. The value of plantations as sources of wood products to meet global demand is therefore well recognized (Fox, 2000; Hagler, 1996; Sedjo, 1999), and species of the genus *Eucalyptus* are now widely planted in many parts of the world to provide wood products. The total area of eucalypt plantation in the world in 2000 amounted to nearly 18 million ha, mainly in South America, South Africa, India, China and South-East Asia (FAO, 2001).

Because of its importance in pulp production worldwide, multi-trait breeding objectives to optimize pulp production from *Eucalyptus* have been developed (Borralho *et al.*, 1993; Greaves & Borralho, 1996; Greaves *et al.*, 1997a; Wei & Borralho, 1999). These studies have concluded that traits that are most strongly positively linked to profitability are wood volume, wood basic density and pulp yield.

Understanding the genetic control of target traits, their relationships, and associated genotype by environment interactions is essential for any tree improvement program. In the work presented here, I studied the genetic control of growth traits, wood basic density and their relationships, and genotype by environment interactions of two of the most widely planted eucalypt species in the tropics, *Eucalyptus urophylla* S. T. Blake and *E. camaldulensis* Dehnh. The possibility of using cellulose content as a selection trait in breeding to improve kraft pulp yields of *E. urophylla* trees was also studied.

1.1 Overview of a tree improvement program

The overall objective of a forest tree improvement program is to develop new plantations that are superior to their predecessors in one or more economically important traits. A breeding program has three main components: testing, selection and mating to form a new generation. From each generation, the benefits are captured by mass propagation of the best currently available genetic material through either seed orchards or vegetative propagation.

To improve a trait substantially through breeding, the trait must be heritable and there must be sufficient genetic variation in the target trait in the population. Therefore, the heritability and coefficient of genetic variation of the trait in the population must be known and quantitatively described.

Genetic correlation refers to the genetic association(s), i.e. strength of the genetic linkage, between two (or more) traits. Genetic correlation between traits may be caused by pleiotropy or linkage disequilibrium (Lynch & Walsh, 1998), and knowledge of both the nature and strength of genetic correlations is highly valuable for predicting the consequences of selection for one trait on other traits in the next generation. Such knowledge is also essential when combining different traits in a multi-trait selection index (Hazel, 1943).

Genotype by environment interaction refers to interactive effects between genetic and environmental factors on the performance of organisms, as manifested in differences in the performance of genotypes among different environments (Falconer & Mackay, 1996). The occurrence of such interaction affects the results of testing and selection in tree improvement programs, and may lead to reductions in overall gains. Hence, knowledge of genotype by environment interactions affecting traits of interest is essential when establishing breeding populations and deployment strategies.

1.2 Natural distribution and biology of the studied species

1.2.1 *Eucalyptus urophylla*

Eucalyptus urophylla S. T. Blake is naturally distributed in Indonesia and Timor-Leste, with extensive native stands on Timor island and throughout Wetar island, with more scattered stands on the nearby islands of Adonara, Alor, Flores, Lomblen, and Pantar (Figure 1). Natural stands of *E. urophylla* are distributed at altitudes ranging from 300 m to about 1100 m in Flores,

Adonara, Alor, Lomblen and Pantar; from 70 m to more than 800 m in Wetar; and from 1000 m up to 2960 m in Timor. *Eucalyptus urophylla* commonly grows on basalt, schists and slates, and rarely on limestone soils (Eldridge *et al.*, 1993). Pryor *et al.* (1995) have suggested that the populations on Wetar, the easternmost island with natural stands of *E. urophylla*, belong to a separate species, *E. wetarensis*, due to differences in their capsule morphology and other traits. However, this newer classification has not been widely accepted internationally (CABI, 2000).

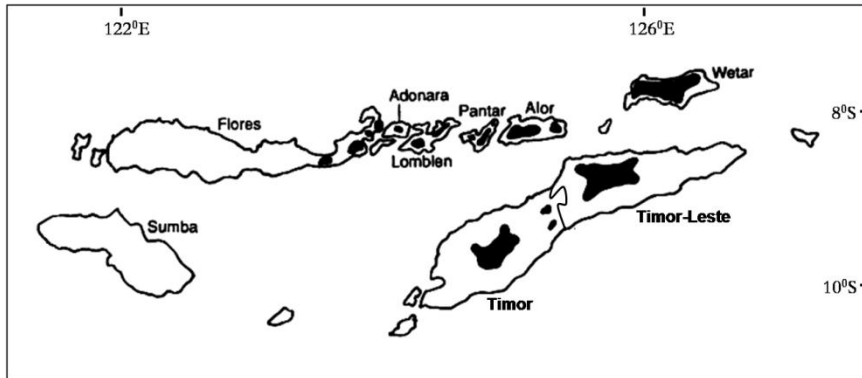


Figure 1. Natural distribution of *Eucalyptus urophylla* (adapted from Eldridge *et al.* 1993)

Eucalyptus urophylla is one of the best eucalypts for planting in low-altitude tropical areas (Jacobs, 1981). Hence, planting areas of this species have increased greatly in regions with humid and sub-humid tropical climates of Africa, Latin America, southern China and South-East Asia since the 1970s (Eldridge *et al.*, 1993). It is planted as a pure species, but has also become very important as a parental species of hybrids, such as *E. grandis* x *E. urophylla* and *E. urophylla* x *E. camaldulensis*, that have displayed excellent hybrid vigor and wider adaptability than the pure-species parents (Kha *et al.*, 2003; McRae, 2003; Turnbull, 1999; Yang, 2003). The plantation-grown wood of *E. urophylla* is mainly used for pulp production, small sawlogs, fuelwood and mining poles, with rotation periods from about six to ten years.

Between-provenance variation in growth rate and wood density in *E. urophylla* has been studied in many countries (Eldridge *et al.*, 1993; Hodge *et al.*, 2001; Kha *et al.*, 2003; Ngulube, 1989; Tripiana *et al.*, 2007; Vercoe & Clarke, 1994; Wei & Borralho, 1998a). These studies have shown that the lower elevation provenances from Flores island generally perform well at low-elevation planting sites. In addition, significant between-provenance variation in wood basic density has been found in South Africa (Darrow &

Roeder, 1983) and Malawi (Ngulube, 1989), where a wide range of provenances have been tested. Ngulube (1989) found that the density tended to decline with increases in altitude of the seed source. However, non-significant differences in wood density have been found between low-elevation provenances tested in China (Wei & Borralho, 1997).

1.2.2 *Eucalyptus camaldulensis*

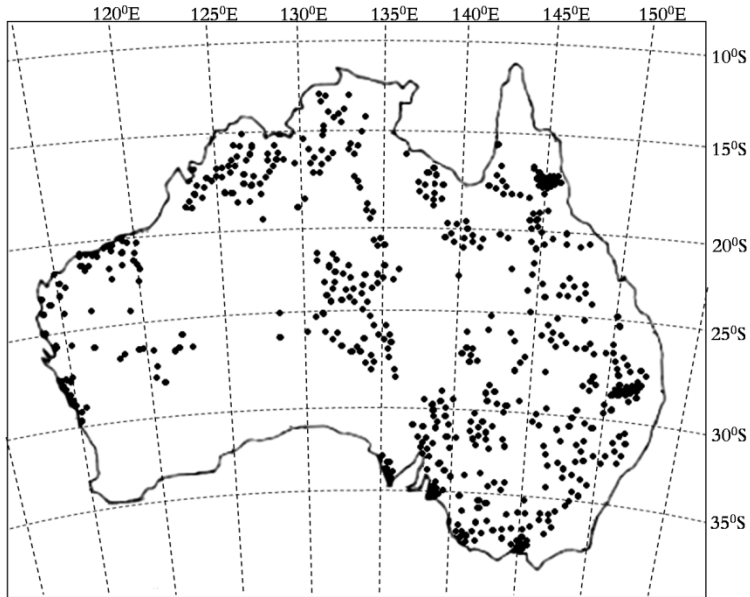


Figure 2. Natural distribution of *Eucalyptus camaldulensis* (adapted from Eldridge *et al.* 1993)

Eucalyptus camaldulensis Dehnh is the most widely distributed eucalypt species, occurring primarily in riverine environments in most dry regions of Australia (Figure 2). Recent taxonomic studies (Brooker & Kleinig, 2004; McDonald *et al.*, 2009) have identified several sub-species of *E. camaldulensis* that are morphologically different, whose distributions are usually geographically distinct, but overlap in some areas. The morphological variation between sub-species has been shown to be closely aligned with genetic differentiation (Butcher *et al.*, 2009). The tropical sub-species occurring in northern Queensland and Northern Territory have proved to be adaptable to a wide range of sub-humid tropical climates, and *E. camaldulensis* has become one of the most widely planted species for pulp and other commercial products in the seasonally dry tropics of many countries (Eldridge *et al.*, 1993), including India, Thailand and Vietnam.

Variation between provenances of *E. camaldulensis* in growth rate, wood properties, drought and salinity tolerance and disease resistance has been reported to be highly significant (Chuong, 1992; Eldridge *et al.*, 1993; Mahmood *et al.*, 2003; Old *et al.*, 2002; Pinyopusarerk *et al.*, 1996; Varghese *et al.*, 2008). Provenances from northern Queensland have reportedly performed well in tropical regions of southern India and South East Asia (Chuong, 1992; Pinyopusarerk *et al.*, 1996; Varghese *et al.*, 2008).

1.3 Genetic improvement of *Eucalyptus* in Vietnam

Eucalypts comprise one of the most important groups of plantation species for the supply of industrial raw materials in Vietnam. The wood is used for pulp and paper, particleboard, construction and furniture-making. Eucalypts have contributed significantly to the improvement of income and living standards of rural people in lowland areas, particularly in central and northern Vietnam. The area of eucalypt plantations in Vietnam at the end of 2001 was estimated to be about 348,000 ha (MARD, 2002). The two main species planted in commercial plantations are *E. urophylla* and *E. camaldulensis*.

Provenance testing of these two species commenced in Vietnam in the 1980s. Good-performing provenances of *E. urophylla* include Lewotobi, Lembata and Egon from Flores island (Kha *et al.*, 2003; Tai, 1994). Good provenances of *E. camaldulensis* include Katherine from Northern Territory and Laura River, Kennedy River and Morehead River from northern Queensland (Chuong, 1992; Kha, 2003). The Petford provenance was previously reported to be promising (Chuong, 1992), but has been severely damaged by defoliation and shoot blight disease, mainly caused by the fungi *Cryptosporiopsis eucalypti* and *Cylindrocladium quinqueseptatum*, particularly in south-east and central Vietnam at sites with a long rainy season and high humidity (Old *et al.*, 2002; Thu *et al.*, 2000).

The first progeny trials of these two species in Vietnam were established in 1996-1997, with two trials of *E. urophylla* in northern Vietnam and one trial of *E. camaldulensis* in the south. The progeny trials were established to be developed into seedling seed orchards to provide seed for commercial plantations, and to serve as base populations for genetic improvement. The genetic materials used in these trials were open-pollinated seeds from about 150 randomly selected mother trees of each species from natural provenances that had proved to be promising in Vietnam and lowland tropical areas in other countries.

In 2000–2001, a total of 150 trees from 60 families were selected from the progeny trial of *E. camaldulensis* in the south, based on family and individual tree performance for growth traits, stem straightness and absence of disease symptoms. These selected trees, together with phenotypically selected trees from commercial plantations, were clonally propagated and used to establish three clonal tests in southern, north–central and northern Vietnam. The purpose of these trials was to select the best clones for clonal deployment and hybrid breeding. The trial in the south was also designed to be converted into a clonal seed orchard by selective thinning, to produce seed for commercial plantations.

In 2005–2008, several open-pollinated progeny trials of *E. urophylla* were established in the north, central lowlands and central highlands of Vietnam, testing 80–220 families at each site. The genetic materials used in these trials were (i) open-pollinated seed of selected trees from the two previous progeny trials in northern Vietnam, (ii) selected trees from seed orchards in Thailand and China, and (iii) trees from natural stands in Indonesia. These progeny trials will be important in Vietnam since they provide a broad genetic base for tree improvement activities and provide information on genotype by environment interactions.

Clonal forestry has been developed for eucalypt species in Vietnam. To date, several clones of *E. camaldulensis* and *E. urophylla* that display good growth and disease resistance have been selected for commercial planting in different areas in Vietnam (FRC, 1998; Nghia, 2007; Thinh *et al.*, 2008).

Eucalypt hybrid breeding has also been developed in Vietnam by producing hybrids of *E. urophylla* x *E. camaldulensis*, *E. urophylla* x *E. exserta*, *E. camaldulensis* x *E. exserta* and, *E. urophylla* x *E. pellita*. Kha *et al.* (2003) found that families of the first three of these hybrid combinations grew 2–3 times more rapidly than their parental species in trials in northern Vietnam. Elite trees of the best performing hybrid combinations have been selected and clonally tested.

1.4 Breeding objectives and important traits in breeding for kraft pulp yield

Eucalypt plantations in Vietnam supply wood for local pulp production for domestic use or woodchips for export to other countries, such as China, Japan and Korea. In Vietnam, there are many plantation growers, including individual farmers, private and state-owned forest companies. These growers usually own small areas of land, and most of them are independent of pulp mills. Individual farmers and small companies sell wood to the pulp and chip

mills through middlemen on a standing volume basis. Some bigger companies have their own chip mills or sell wood at the mill gate on a green weight basis. As a result, breeding objectives and the relative importance of objective traits can vary, depending on who is guiding the breeding program.

Wei and Borralho (1999) discussed three production systems involving eucalypt plantations in south-east China that had substantially differing breeding objectives: (i) pulp production, in which the primary objective is to minimize costs per unit of pulp produced; (ii) woodchip production, in which the objective is to minimize costs per unit dry weight of wood; and (iii) standing volume production, in which the objective is to maximize the benefit of standing volume per hectare of plantation. The relative importance of objective traits varies in these systems, e.g. pulp yield is important in pulp production, but not in woodchip or standing volume production, while density is important in pulp and woodchip production, but not in standing volume production. However, there are strong positive relationships between the objectives (Wei & Borralho, 1999), indicating that selection for any breeding objective is likely to result in substantial gains in other objectives. Currently, the woodchip and standing volume production systems are dominant in Vietnam, but the situation may change in the future when some new pulp mills start operating. Therefore, breeding objectives of eucalypt plantations in Vietnam should either be to reduce costs per unit dry weight of wood or to maximize the benefit of volume per hectare of plantation. However, either should maintain acceptable pulp yields for future Vietnamese pulp mills.

Objective traits are those traits that influence the breeding objective directly. As mentioned above, the objective traits that are most strongly positively linked to profitability of a pulpwood breeding objective are wood volume, wood basic density and pulp yield, i.e. pulp productivity = volume x basic density x pulp yield. Their relative importance in kraft pulp production is discussed below.

Wood volume is the most important trait, and the key determinant of profitability of plantations, provided that basic density and pulp yield are within acceptable ranges. An increase by a unit of coefficient of additive genetic variation ($CV_A\%$) for volume often gives greatest gain in term of reduction cost for pulp production compared to corresponding increase in wood density and pulp yield (Greaves *et al.*, 1997a; Wei & Borralho, 1999).

Wood basic density influences many processes in the production chain, and within the range of basic density typical of short-rotation plantation eucalypts, increases in density will reduce the cost of pulp production

(Greaves & Borralho, 1996; Greaves *et al.*, 1997a; Wei & Borralho, 1999). Greaves & Borralho (1996) found that an increase of 10% in density would decrease total pulping costs per ton of eucalypt kraft pulp by approximately 5%. However, the relationships between wood density and other pulp and paper properties are not well understood. Dean (1995) reported that the most suitable range of wood basic density in eucalypts for pulpwood production was between 470 kg m⁻³ and 550 kg m⁻³, and that pulp yields declined sharply when basic density exceeded 600 kg m⁻³ or fell below 400 kg m⁻³.

Pulp yield is defined as the oven-dry weight of pulp per unit oven-dry weight of wood (Smook, 1982). In terms of production costs per ton of pulp, pulp yield affects all processes in the production chain (Greaves & Borralho, 1996; Greaves *et al.*, 1997a; Wei & Borralho, 1999). Greaves and Borralho (1996) found that an increase of 10% of the mean value would reduce total pulping costs by 7%, excluding reductions in costs of plantation establishment, maintenance, harvesting and freight associated with increased pulp yields.

Ideally, selection should be based on the objective traits. However, these objective traits are expressed at harvesting (full rotation) and are difficult and/or expensive to measure. Therefore, to increase the rate of genetic gain from breeding and reduce costs, selection is usually based on selection traits that are correlated with the objective traits and are measured on younger trees. Selection traits that are typically used in pulpwood breeding programs are young-age diameter at breast height (linked to harvest volume) and basic density of a breast-height wood core, or pilodyn penetration (linked to whole-tree basic density at harvest). Some programs have used pulp yield or cellulose content predicted/determined from a breast-height wood sample as selection traits for whole-tree pulp yield at harvest (McRae *et al.*, 2004).

1.5 Genetics of growth traits and wood properties in *Eucalyptus*

1.5.1 Genetic parameters for growth traits

Generally, growth traits of forest trees have low to moderate heritability and high CV_A values (Cornelius, 1994). Narrow-sense heritabilities of growth traits in some eucalypt species are presented in Table 1, showing a median of 0.20 and values mostly ranging from 0.10 to 0.30. Coefficients of additive genetic variation are in the range of 7% to 13% for diameter and height (Apiolaza *et al.*, 2005; Gapare *et al.*, 2003; Hamilton & Potts, 2008).

Table 1. Reported heritability values of growth traits and wood properties of some commercial *Eucalyptus* species

Species	h^2	Age	Reference
Growth traits			
<i>E. urophylla</i>	0.20–0.49	3–5	Wei & Borralho (1998a)
<i>E. urophylla</i>	0.13	3	Arnold & Cuevas (2003)
<i>E. camaldulensis</i>	0.06–0.20	2	Pinyopusarek <i>et al.</i> (1996)
<i>E. camaldulensis</i>	0.08–0.19	2	Varghese <i>et al.</i> (2008)
<i>E. camaldulensis</i>	0.11–0.14	5	Mahmood <i>et al.</i> (2003)
<i>E. camaldulensis</i>	0.24–0.62 [†]	3	Varghese <i>et al.</i> (2008)
<i>E. grandis</i>	0.08–0.21	4.5	Floyd <i>et al.</i> (2003)
<i>E. grandis</i>	0.09–0.52 [†]	6	Osorio <i>et al.</i> (2001)
<i>E. globulus</i>	0.15–0.33	7–8	Raymond <i>et al.</i> (2001)
<i>E. globulus</i>	0.16–0.32	4–6	Costa e Silva <i>et al.</i> (2006)
<i>E. nitens</i>	0.24–0.39	-	Reviewed by Hamilton & Potts (2008)
Wood density			
<i>E. urophylla</i>	0.71	6	Wei & Borralho (1997)
<i>E. camaldulensis</i>	0.67 [†]	3	Varghese <i>et al.</i> (2008)
<i>E. grandis</i>	0.29–0.42 [†]	6	Osorio <i>et al.</i> (2001)
<i>E. globulus</i>	0.50–0.80	8–9	Borralho <i>et al.</i> (1992)
<i>E. globulus</i>	0.67–1.00	7–8	Raymond <i>et al.</i> (2001)
<i>E. globulus</i>	0.44	11	Apiolaza <i>et al.</i> (2005)
<i>E. nitens</i>	0.11–0.96	-	Reviewed by Hamilton & Potts (2008)
Cellulose content			
<i>E. globulus</i>	0.32–0.57	7–8	Raymond & Schimleck (2002)
<i>E. globulus</i>	0.84	11	Apiolaza <i>et al.</i> (2005)
<i>E. nitens</i>	0.37–1.00	-	Reviewed by Hamilton & Potts (2008)
Pulp yield			
<i>E. globulus</i>	0.33–0.58	7–8	Raymond <i>et al.</i> (2001)
<i>E. globulus</i>	0.43	11	Apiolaza <i>et al.</i> (2005)
<i>E. nitens</i>	0.03–0.79	-	Reviewed by Hamilton & Potts (2008)

[†] Clonal repeatability

Genetic parameters for wood density

Wood density is by far the most intensively studied wood quality trait. Reported heritabilities of wood density in eucalypts range from 0.29 to 1 (Table 1), with a median value of 0.67, agreeing well with values for most forest tree species (Cornelius, 1994). In addition, according to a review of eucalypts (Raymond, 2002), heritability appears to be higher for wood density than for other commonly measured wood property traits (wood

density, pulp yield and fiber length) in *E. globulus* and *E. nitens*. There is little information on CV_A in wood density in eucalypts, but in his review of a wider range of species, Cornelius (1994) found a median CV_A for wood density of 5.1%, while values for height and diameter were 8.1–8.6%.

Genetic parameters for cellulose content and pulp yield

The genetic control of cellulose content and pulp yield has been studied in two eucalypts, *E. globulus* and *E. nitens*, in which moderate to high heritability of these traits has been found (Table 1). It should be noted that the reported results regarding pulp yield and cellulose content in these studies were based on near infrared reflectance (NIR). Some authors have reported similar heritability for both cellulose content and pulp yield (Raymond *et al.*, 2001; Raymond & Schimleck, 2002). In contrast, others have found higher heritability for cellulose content; the mean heritability of cellulose content in these studies was 0.63, whereas the mean value for pulp yield was 0.43 (Kube *et al.*, 2001; Raymond *et al.*, 2001; Raymond & Schimleck, 2002; Schimleck *et al.*, 2004; Tibbits & Hodge, 1998). Reported CV_A values for cellulose content and pulp yield range from 2% to 3% (Apiolaza *et al.*, 2005; Kube *et al.*, 2001; Raymond *et al.*, 2001).

Genetic correlations between traits

Genetic correlations between growth traits and wood density in eucalypt species are often unfavorable, but their strength varies between studies (Table 2). Generally, estimated correlations have had large standard errors and appear to be non-significant. Genetic correlations between cellulose content or pulp yield and growth traits or density have only been published for *E. globulus* and *E. nitens*, and have ranged from -0.53 to 0.86 (Table 2) in different studies, often with large standard errors.

Variations in estimates of trait-trait genetic correlations within a species may be due to differences in the populations examined in different studies (Falconer & Mackay, 1996). Variation has also been found when examining the same genetic materials allocated in different environments (Raymond & Schimleck, 2002). In addition, relatively small sample sizes have often been used to estimate genetic correlations between growth traits and wood properties or between different wood properties, which reduces the precision of estimates.

Table 2. Reported genetic correlations (r_G) between traits in some commercial Eucalyptus species

Trait 1	Trait 2	Species	r_G	Reference
Diameter	Density	<i>E. urophylla</i>	-0.36	Wei & Borralho (1997)
			-0.04	Ignacio-Sánchez <i>et al.</i> (2005)
		<i>E. globulus</i>	-0.58	Apiolaza <i>et al.</i> (2005)
		<i>E. globulus</i>	-0.44 to 0.00	Raymond & Schimleck (2002) (from 3 sites)
		<i>E. nitens</i>	-0.79 to 0.08	Reviewed by Hamilton & Potts (2008) (from 9 studies)
Diameter	Cellulose content	<i>E. globulus</i>	-0.51 to -0.11	Raymond & Schimleck (2002) (from 3 sites)
		<i>E. globulus</i>	0.61	Apiolaza <i>et al.</i> (2005)
		<i>E. nitens</i>	0.25 to 0.86	Reviewed by Hamilton & Potts (2008) (from 5 studies)
Density	Cellulose content	<i>E. globulus</i>	0.61	Apiolaza <i>et al.</i> (2005)
		<i>E. globulus</i>	-0.33 to 0.67	Raymond & Schimleck (2002) (from 3 sites)
		<i>E. nitens</i>	-0.53 to 0.37	Reviewed by Hamilton & Potts (2008) (from 5 studies)
Density	Pulp yield	<i>E. globulus</i>	0.0 to 0.74	Raymond & Schimleck (2002) (from 3 sites)
		<i>E. nitens</i>	0.42	Kube & Raymond (2002)

Age-age genetic correlations can also be estimated, between a trait measured at one age and the same trait measured at other ages. A high and positive genetic correlation between measurements at an earlier and later age indicates that it may be efficient to carry out selection at an early age and hence reduce breeding turnover. In the short rotation plantations of tropical eucalypts, genetic correlations between earlier and rotation-end measurement for growth traits are usually strong (Marques *et al.*, 1996; Osorio *et al.*, 2003; Wei & Borralho, 1998a), suggesting that selections can be made as early as at ages of one to three years.

There have been few publications describing age-age genetic correlations for wood density in eucalypts (Greaves *et al.*, 1997b; Osorio *et al.*, 2003), but strong age-age genetic correlations have been found. The genetic correlations between basic density at ages of 3 years and 6 or 7 years ranged from 0.71 to 0.95 in these studies, indicating that early selection is efficient for wood density.

Genotype by environment interactions

Genotype by environment interaction has commonly been found to be strong for growth traits in eucalypts (Mahmood *et al.*, 2003; Mori *et al.*, 1988; Pinyopusarerk *et al.*, 1996; Raymond *et al.*, 2001; Santos, 1990; Varghese *et al.*, 2008). In contrast, the interactions are generally less important for wood density, cellulose content and pulp yield (Kube *et al.*, 2001; MacDonald *et al.*, 1997; Raymond, 2002; Raymond *et al.*, 2001; Wei & Borralho, 1997). These results have some important implications for tree improvement programs, notably: (i) for growth traits, genotypes must be extensively tested across different sites in the target areas to select the best genotypes for each type of site or good average genotypes; (ii) testing of wood density and pulp yield can be limited to one or few sites and only minor interactions for these traits at other sites is expected.

2 Objectives

The overall objective of the studies this thesis was based upon was to increase knowledge regarding the genetic control of economically important traits in *Eucalyptus urophylla* and *E. camaldulensis* in order to support the development of tree improvement programs in Vietnam. For this purpose, I estimated: (i) genetic parameters of growth traits, stem straightness, branch size, wood basic density and cellulose content; (ii) age-age genetic correlations and optimum selection ages; (iii) genetic correlations between traits; (iv) genotype by environment interactions for these traits; and (v) selection gains and correlated responses for several selection strategies that could be applied in *E. urophylla* breeding and *E. camaldulensis* deployment programs.

3 Materials and Methods

The *Eucalyptus urophylla* studies focused on the two progeny trials in northern Vietnam, at Ba Vi and Van Xuan (Figure 3). In each trial 144 open-pollinated families from nine natural provenances were being tested (Paper I, Table 1). The two trials are located at sites 60 km away from each other, with similar soil and climatic conditions that are typical for low hill-side areas in northern Vietnam.

The *E. camaldulensis* study focused on the three clonal tests established at Ham Thuan Nam in southern, Dong Hoi in north-central and Ba Vi in northern Vietnam (Figure 3). Individual trials were testing 90 to 120 clones and a total of 172 clones were represented in one or more of the three trials (Paper V, Table 1).

Details of trial locations, site conditions, and experimental design are provided in Paper I, Table 2 and Paper V, Table 3. The number of families or clones sampled, traits measured and ages of assessments in the studies described in each paper are summarized in Table 3. Stem straightness and branch size were recorded in 5-class scales (I). Wood basic density was determined using 5 mm cores



Figure 3. Locations of *Eucalyptus urophylla* and *E. camaldulensis* trials used in our studies.

taken at breast height in the progeny trials of *E. urophylla*, either entire cores or radial segments to study age-age genetic correlations. In the clonal trials of *E. camaldulensis*, density was determined using 5 cm disks taken from felled trees. Wood basic density was measured by the water displacement method (Olesen, 1971). Wood density was also measured indirectly in terms of ‘Pilodyn penetration’ i.e. the depth of penetration into the wood of a pin projected by Pilodyn equipment. Cellulose content was determined by the diglyme-HCl method (Wallis *et al.*, 1997), and lignin content by a modified acetyl bromide method (Iiyama & Wallis, 1988).

Table 3. Numbers of families or clones sampled in each trial, ages of assessments and traits measured in the studies described in each paper

Species/ Trial	Number of families or clones sampled	Traits studied	Age (Years)	Paper
<i>Eucalyptus urophylla</i>				
Van Xuan	144 families	Diameter, height	1-9	I
		Stem straightness, branch size	5,9	I
		Density, pilodyn penetration	9	II
Ba Vi	127-144 families	Diameter, height	1-8	I
		Stem straightness, branch size	5, 8	I
	127 families	Density, pilodyn penetration	8	II
	11 families	Cellulose & lignin content	8-9	III
	62 families	Density, cellulose content, pulp yield	10	IV
<i>Eucalyptus camaldulensis</i>				
Ham Thuan Nam	100 clones	Diameter, height	1-5	V
		Density, pilodyn penetration	5	V
Dong Hoi	120 clones	Diameter, height	1-5	V
		Density, pilodyn penetration	5	V
Ba Vi	90 clones	Diameter, height	1-3	V
		Density, pilodyn penetration	3	V

Subsequent statistical analysis of the acquired data was based on a mixed linear model and conducted in two steps: (i) multivariate analysis of data gathered on materials at single sites, in which variance components for each trait and covariances between traits were estimated; (ii) multivariate across-site analysis in which genetic correlations between sites were estimated. Genetic parameters were calculated based on estimated variances and covariances. A selfing rate of 10% in the natural stands of *E. urophylla* (Gaioto *et al.*, 1997; House & Bell, 1994) was assumed to estimate narrow-sense within-provenance heritabilities of traits in progeny trials of this species.

4 Main results and discussion

4.1 Genetic control of economically important traits

Significant differences were found in growth, stem straightness and branch size between provenances of *E. urophylla* tested at two sites (Paper I, Table 3). The Lewotobi provenance grew significantly better than all other provenances, and had the best stem straightness and acceptable branch size at both sites. The differences in growth among other provenances were generally not significant. Wood basic density (DEN) and cellulose content (CC) were not significantly different between provenances (Paper II, Table 3; and paper IV, Table 3). These results suggest that provenance selection will be effective for improving growth, stem straightness and branch size of *E. urophylla*, but not for wood density or pulp yield.

In *E. urophylla*, narrow-sense within-provenance heritabilities for growth traits were 0.20 on average (Table 4), and the heritability of growth traits increased with age (Paper I, Figure 1). The trend of increasing heritability was clearer for diameter at breast height (DBH), whereas it was relatively stable for height (HT) from ages of two years onward. Coefficients of additive genetic variation remained stable at different ages for both DBH and HT (Paper I, Table 4). Heritability and CV_A estimates for DEN were about 0.60 and 6.3%, respectively (Table 4). Pilodyn penetration (PP), which was used as an indirect measure of DEN, had lower heritability but similar CV_A to DEN (Paper II, Table 4). Cellulose content had a heritability of 0.50 and CV_A of 3.9% (Paper IV, Table 3). It should be noted that these genetic parameters were estimated in selectively thinned progeny trials of *E. urophylla*. The longitudinal multivariate analysis approach (Apiolaza *et al.*, 2000) with relationship matrix as a central role (Wei & Borralho, 1998b) has been applied to reduce effect of thinning in estimation of genetic parameters for growth traits (paper I). The selective thinning is unlikely to have heavily

affected the estimation of genetic parameters for wood density and cellulose content, as discussed in Papers II and IV.

In the three clonal trials of *E. camaldulensis* at Ham Thuan Nam (south Vietnam), Dong Hoi (north-central Vietnam) and Ba Vi (north Vietnam), average clonal repeatabilities for growth traits were about 0.28 (Table 4), and increased with age (Paper V, Table 5). The coefficients of genetic variation (CV_G) for growth traits remained stable with age at each site (Paper V, Table 5). Wood basic density had similar repeatabilities (0.71–0.78) and CV_G (5.1–6.7%) at all three sites. Pilodyn penetration showed lower repeatabilities (0.56–0.66), but higher CV_G (6.6–8.0%) than DEN (Paper V, Table 5).

These results indicate that there are substantial degrees of genetic control for growth traits, stem straightness, branch size, wood density and cellulose content in open-pollinated populations of *E. urophylla*; and for growth traits and wood density in clonal populations of *E. camaldulensis* in Vietnam. These findings suggest that considerable genetic improvement can be achieved in eucalypt plantations for pulp production in Vietnam through *E. urophylla* breeding programs or clonal deployment of *E. camaldulensis*.

Table 4. Average within-provenance narrow-sense heritability (h^2), clonal repeatability (H_C^2), coefficient of additive genetic variation (CV_A) and coefficient of genetic variation (CV_G) for traits studied in *Eucalyptus urophylla* and *E. camaldulensis*

Trait	Description	<i>E. urophylla</i>		<i>E. camaldulensis</i>	
		h^2	CV_A	H_C^2	CV_G
DBH	Diameter at breast height	0.20 ^t	10.3 ^t	0.28 ^t	13.5 ^t
HT	Height	0.20 ^t	9.7 ^t	0.28 ^t	9.7 ^t
STR	Stem straightness	0.19 ^t	-	-	-
BRA	Branch size	0.13 ^t	-	-	-
CC	Cellulose content	0.50	3.9	-	-
DEN	Wood basic density	0.60	6.3	0.75	6.1
PP	Pilodyn penetration	0.42	5.0	0.62	7.7

^tAverage value at different ages and sites

4.2 Age-age genetic correlations and optimum selection ages

In *E. urophylla*, age-age genetic correlations became stronger with decreasing differences between ages of measurement for both DBH and HT, ranging from 0.30 to 0.97 for DBH, and from 0.27 to 0.97 for HT (Paper I, Table 5). Genetic correlations between measurements at 3 years of age and final measurement were strong ($r_g > 0.70$) for both DBH and HT. Genetic

correlations between DEN of the segment near the pith and the total core were strong, and indicated that selection for wood density can be effective at approximately 3 years of age (Paper II, Table 6).

Given a 2-year time lag for breeding activities and identical selection intensity, the efficiency of early selection generally increased to a maximum between ages of 2 and 4 years, depending on rotation age. For a 5-year rotation (mainly for pulpwood) selection efficiency was maximized after 2 years for HT and after 3 years for DBH (Paper I, figure 3a). For a rotation time of 10 years, selection efficiency peaked after 3 years for both DBH and HT (Paper I, Figure 3b). Generally, selection efficiency reached an optimum at about 1/3 of the anticipated plantation rotation period.

In *E. camaldulensis*, genotypic correlations between measurements of growth traits at earlier ages and final measurement (at 5 years of age) at Ham Thuan Nam and Dong Hoi were generally high. Genotypic correlations between measurements of growth traits at ages of 2 and 5 years ranged from 0.84 to 0.89 at all sites (Paper V, Table 7). The results suggest that the best performing clones for deployment can be selected at ages as early as 2 years.

4.3 Relationships between traits

In *E. urophylla*, genetic correlations between DEN and growth traits ranged from 0.10 to 0.28 (Paper II, Table 5). The correlation between CC and DEN was -0.02, and that between CC and growth traits ranged from 0.28 to 0.45 (Paper IV, Table 4). All estimated genetic correlations had large standard errors and did not differ significantly from zero.

The phenotypic correlation between DBH and CC, and between DBH and DEN in *E. urophylla* was 0.58 and -0.50, respectively (Paper III, Table 3). Both correlations were significant ($p < 0.001$). The phenotypic correlations between lignin content and CC, DEN, and DBH, between CC and DEN were weak and not significant (Paper III, Table 3). The significant phenotypic correlation between CC and DBH and similarity with its genetic correlation may suggest an existing genetic relationship between them (cf. Lynch & Walsh, 1998). These findings suggest that there is no obstacle to combine high growth rate with high CC for *E. urophylla* plantations grown for pulp production.

In *E. camaldulensis*, genotypic correlations between growth traits and DEN varied from -0.24 to 0.21 at all three sites and did not differ significantly from zero (Paper V, Table 8).

In both species, genetic or genotypic correlations between DEN and PP were strong, ranging from -0.86 to -0.95, and highly significant

($p < 0.001$) (Paper II, Table 5 and Paper V, Table 8). The correlation is negative since a high value for penetration corresponds to a low density. The results suggest that PP can be used as a reliable proxy for DEN measurements in both *E. urophylla* and *E. camaldulensis* improvement programs.

4.4 Genotype by environment interactions

Genetic correlations between the two progeny trials of *E. urophylla* in northern Vietnam, where the soil and climatic conditions are similar, were strong and stable from ages of 3 years ($r_G > 0.8$) for growth traits (Paper I, Table 9), and for DEN (0.89) at 8 years (Paper II, Table 4).

In *E. camaldulensis*, genotypic correlations between sites in southern, north-central and northern Vietnam varied from 0.32 to 0.59 for growth traits, and from 0.72 to 0.88 for density, as determined by either direct (DEN) or indirect (PP) measurements (Paper V, Table 8). Log-likelihood ratio tests indicated that all genotypic correlations were significantly different from 1. Genotypic correlations between different pairs of sites did not differ statistically from one another, for any of the traits. These results suggest that different sets of clones should be used in different regions to maximize selection gains in growth, whereas ranking of clones will vary little across sites for density.

Growth of *E. camaldulensis* clones differed significantly in their stability of growth across different sites. Among 32 clones that were planted at all three sites, only 11 (30% of the clones) contributed significantly to total interaction variance in DBH (Paper V, Figure 1). This finding suggests that it should be possible to select clones that perform well at all sites.

4.5 Selection gains and correlated responses

Table 5. Selection gains and correlated responses in *Eucalyptus urophylla* using average genetic parameters from final measurements at a selection proportion of 1% (see Table 4 for meanings of abbreviations)

<i>Eucalyptus urophylla</i>	h^2	CV_A (%)	Selection gain (%)	Correlated response		
				DBH (%)	DEN (%)	CC (%)
DBH	0.29	10.5	15.1	-	2.6	2.6
DEN	0.60	6.3	13.0	5.9	-	-0.1
PP	0.42	5.0	-8.7	4.3	9.3	-
CC	0.50	3.9	7.4	8.7	-0.3	-

In *E. urophylla*, the selection gains from breeding at a 1% selection proportion (corresponding to selection of the 15 best trees from the two progeny trials, in which there were about 1500 trees, in total) were 15.1% for DBH, 13.0% for DEN and 7.4% for CC (Table 5). The selection gain in DBH would correspond to a selection gain of 28.3% in volume according to the genetic parameters estimated in Paper IV. Selection for DBH alone resulted in increases of 2.6% of mean values in both DEN and CC. Selection for DEN or CC alone resulted in 5.9–8.7% increases in DBH, equivalent to 40–60% of the potential increase that could be obtained by selecting for DBH alone.

Table 6. Selection gains and correlated responses from clonal deployment of *Eucalyptus camaldulensis* using average genetic parameters at final measurement and a selection proportion of 5% (see Table 4 for meanings of abbreviation)

Traits	H_C^2	CV _g (%)	Selection gain (%)	Correlated responses	
				DBH (%)	DEN (%)
DBH	0.36	14.6	26.3	-	-1.0
DEN	0.75	6.1	12.5	-2.2	-
PP	0.62	7.7	-16.3	-5.5	11.3

In *E. camaldulensis*, selection gains from deployment of the best 5% of clones (corresponding to selection of the best five clones from a population of 100 clones) were 26.3% for DBH and 12.5% for DEN. Selection for DBH alone would decrease DEN by 1%. Selection for DEN or PP alone resulted in DBH decreasing by 2.2% to 5.5%, respectively (Table 6). The selection for DBH, based on results at one site at a 5% selection proportion, gave indirect responses in DBH ranging from 11.8% to 13.2% at the other two sites (Paper V, Table 10). This accounted for only 40–60% of the potential gains that could be obtained from direct selection at individual sites. The results further confirm the suggestion that different set of clones should be used at each site to ensure maximum selection gains in growth. Another way to manage genotype by environment interactions is to select good, stable clones for deployment across sites. As an example, use of three fast-growing and stable clones (10% of the clones present at all three sites) resulted in selection gains in DBH of 80–95% compared to the gain achieved by selection at individual sites at a 10% selection proportion (V).

In both species, selection relying on PP resulted in 70–90% of the potential gain obtained from direct measurement of DEN. The results show that PP can be reliably used as an indirect measurement of DEN, either for breeding *E. urophylla* or clonal deployment of *E. camaldulensis*.

5 Implications for tree improvement

5.1 Objective traits and selection traits

In the sections below, the efficiency of PP and CC as selection traits for wood density and pulp yield are discussed. For wood volume, diameter and height are used as selection traits.

Ideally, selection to maximize gains in wood density should be based on direct measurements of this variable, but it is difficult to measure wood density directly in operational breeding, especially when screening large numbers of genetic entries because it is rather expensive and time-consuming. However, pilodyn penetration can be used to obtain quick, simple, cost-effective indirect measurements of wood density (Greaves *et al.*, 1996). Results from the studies this thesis is based upon indicate that PP is under strong genetic control and its coefficient of genetic variation is similar to that of DEN in both *E. urophylla* and *E. camaldulensis*. Furthermore, genetic or genotypic correlations between DEN and PP ranged from -0.86 to -0.95, and selection gains in DEN based on selection for PP amounted to 70-90% of those achievable by direct selection for DEN. These results suggest that PP can be used as a selection trait for wood density in either breeding or clone deployment of both *E. urophylla* and *E. camaldulensis*.

We found CC to be strongly correlated with pulp yield in *E. urophylla*, and thus it could be used as a selection trait in breeding to increase pulp yields. The estimated selection gain (percent of mean value) in CC was 7.4%, at a 1% selection proportion, which is equivalent to a 4.2% increase (percent of mean value) in pulp yield based on the relationship between CC and pulp yield estimated in Paper IV. This result is similar to the selection gains for pulp yield in *E. globulus* calculated from parameters reported by Raymond *et al.* (2001), which ranged from 3.4 to 5.8% at the same selection intensity, based on measurements of pulp yield by NIR spectrometry. The

method applied to determine CC in our study is simple and non-destructive, but still time-consuming which would hinder its use for screening many trees. In the future, use of NIR-calibrated prediction of CC is recommended. Calibration curves can be developed using samples that have been chemically analyzed for CC, and such calibrations have enabled accurate predictions of CC using NIR spectroscopy in *E. globulus* and *E. nitens* (Raymond & Schimleck, 2002; Schimleck *et al.*, 2004).

5.2 Suggestions for *Eucalyptus* tree improvement for pulp production in Vietnam

In Vietnam, *E. urophylla* is one of the most widely planted species for commercial plantations because of its good performance in the north, central lowlands and sites at lower elevations in the central highlands. Therefore, an intensive genetic improvement program for this species is needed to maximize benefits with respect to defined breeding objectives.

The growth rate of the trees we examined was relatively slow compared to those observed in other countries. Annual mean height growth of *E. urophylla* in our studies was in the range 2–3 m, compared with reported rates of 3–5 m per year in China and Brazil, where growing conditions are more favorable (Santos, 1990; Wei & Borralho, 1998a). Clearly, genetic improvement of eucalypt plantations in Vietnam should focus on increasing growth performance, but with generally degraded and low fertility soils available for planting, and cool and dry winter in the north, growth rates will remain below those in many other countries.

As mentioned above, standing volume and wood chip production systems (Wei & Borralho, 1999) dominate in Vietnam. Results from our study indicate that the CV_A value for CC is low, in accordance with findings of other studies (Apiolaza *et al.*, 2005; Costa e Silva *et al.*, 2009; Greaves *et al.*, 1997a; Raymond *et al.*, 2001), suggesting that pulp yield may be difficult to improve substantially through breeding. Further, increasing pulp yield has received less emphasis as a breeding objective for kraft pulp production than increasing wood volume and density (Greaves *et al.*, 1997a; Wei & Borralho, 1999). Therefore, the selection strategy should focus on improving growth and density while maintaining acceptable pulp yield for pulp production.

Since economic weights for objective traits have not yet been estimated for eucalypts grown under Vietnamese conditions an independent culling selection method should be applied in current selections, to ensure that pulp yield does not fall below acceptable levels. The genotypic values obtained

for DBH, DEN and CC of the 275 trees examined in the study described in Paper IV, using the best linear unbiased prediction (BLUP) method (Figure 4), were used to illustrate the likely efficacy of independent culling. Approximately 1% of the trees in the sample population were among the best 5% in terms of DBH and DEN, but still had CC values that were higher than the population mean value.

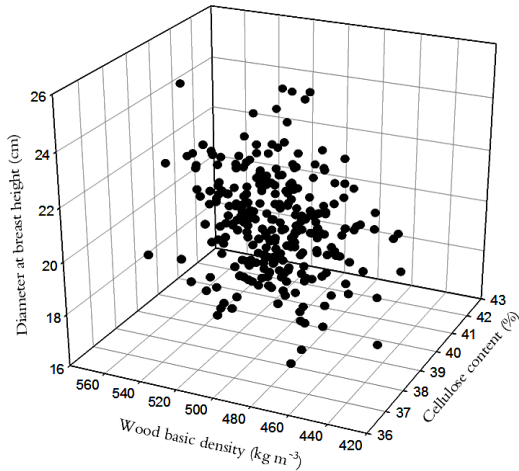


Figure 4. Best linear unbiased predictions of genotypic values of 275 *E. urophylla* trees at Ba Vi for diameter at breast height, wood basic density and cellulose contents.

Genetic correlations between the two progeny trials of *E. urophylla* in northern Vietnam were strong for both growth and wood density (Papers I and II). However, plantation areas of *E. urophylla* in Vietnam extend from the north to central Vietnam and lower elevation areas in the central highlands. These areas differ substantially in both edaphic (Chieu & Thuan, 1996) and climatic conditions (Dac & Toan, 1993). Therefore, further evaluations of genotype by environment interactions affecting the performance *E. urophylla* across planting areas of this species in Vietnam are needed. In a recent study, genetic correlations between the other two progeny trials of *E. urophylla*, established at Ba Vi in the north and Dong Ha (latitude: 16^o50'N, longitude: 107^o05'N) in north-central Vietnam, at age 3 years were found to vary from 0.31 to 0.39 for DBH and HT, respectively, and 0.93 for PP (Kien, unpublished data). These findings suggest that the growth performance of *E. urophylla* in northern and north-central Vietnam is subject to strong genotype by environment interactions. Therefore, different breeding populations should be allocated in different ecological areas in Vietnam, and breeding activities should be carried out within each

population to maximize genetic gain in growth in each area. Further study is needed to determine the minimum number of breeding populations of *E. urophylla* that should be maintained in Vietnam.

The progeny trials of *E. urophylla* used in our study are currently used as genetic resources for the tree improvement program in northern Vietnam. However, in order to maintain a broad genetic base for long-term tree improvement, it is important to incorporate new and unrelated genetic entries from other sources to increase genetic diversity in the breeding populations.

Clonal forestry often practiced when *E. urophylla* is grown commercially since it is easy to propagate vegetatively. The selected trees can be vegetatively propagated and clonally tested at different sites in the targeted regions to select good clones for each region. It may be also possible to select clones of *E. urophylla* with desirable traits that are stable across sites, as demonstrated in our *E. camaldulensis* study. The strategy in which good and stable clones are deployed in multi-clonal stands may be more appropriate in Vietnam, where management of individual clones is difficult for most small plantation growers and nursery owners. However, this strategy may end up with limited number of clones that are commercially planted in a large scale. Therefore, many clones should be tested to select sufficient number of clones for planting across regions to maintain acceptable levels of genetic diversity in the plantations.

Eucalyptus camaldulensis is an important planting species in southern Vietnam in areas with low mean annual rainfall (< 1400 mm) and a long dry season. However, commercial plantations of *E. camaldulensis* in northern and north-central Vietnam are not extensive because growth of this species is poorer than that of *E. urophylla* in these regions (Kha, 2003). Therefore, breeding and deployment of *E. camaldulensis* should focus on southern Vietnam. Clones that display good growth at the trial site in the south are expected to be well adapted to these conditions, and can therefore be used for commercial planting and further breeding in the region. The best performing clones selected in northern and north-central Vietnam could be used in hybrid breeding programs with *E. urophylla* and perhaps other eucalypt species to produce inter-specific hybrid combinations targeted to these regions.

6 Future perspectives

Inter-specific hybrid breeding and clonal forestry using elite hybrid clones have been successfully developed for eucalypt plantations in many countries. Hybrid breeding to develop clones with both fast growth and desired wood quality could bring substantial economic benefits for Vietnam.

In order to develop an appropriate tree improvement program, knowledge of the relative importance of objective traits is very important. Therefore, further bio-economic studies to determine the economic weights of important objective traits under different production systems are needed.

Further study of genotype by environment interactions in *E. urophylla* across a wider range of environments is needed to determine whether different breeding populations are required for different planting regions in Vietnam. A cost-effective alternative would be to test and select clones that are well-adapted to different regions while relying on a single breeding population. Depending on the degree of genotype by environment interaction that is present, this alternative may achieve much or most of the selection gain that would be obtained from a strategy involving use of different breeding populations in the contrasting environments.

The three clonal trials of *E. camaldulensis* covered a wide range of environments, but did not test the clones in a strongly disease-prone environment, and this is recommended. Breeding for increased volume, pulp yield and disease resistance in *E. camaldulensis* should be considered, for both pure species development and hybrid breeding. The incidence and severity of disease attacks should be evaluated both at different sites and at various times throughout the lifetimes of plantations.

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