A quantitative study on growth, basic wood density and pulp yield in a breeding population of *Eucalyptus urophylla* S.T. Blake, grown in KwaZulu-Natal

by

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Declaration

I hereby certify that this thesis is the result of my own investigations unless specifically indicated in the text and has not been submitted for a higher degree at any other institution.

Signed……..

Francois van Deventer

I hereby certify that this statement is correct.

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In memory of Eric Kietzka and Errol Duncan whom taught me nearly everything I know about tree breeding.

A quantitative study on growth, basic wood density and pulp yield in a breeding population of *Eucalyptus urophylla* S.T. Blake, grown in KwaZulu-Natal

Abstract

The first objective of this study was to evaluate *Eucalyptus urophylla* S.T. Blake provenances in terms of their growth, basic wood density and pulp yield properties. The second objective was to determine the genetic and phenotypic associations that may exist between growth, basic wood density and pulp yield.

Data of 9022 open-pollinated progenies representing 306 families, collected from 17 provenances, were used to evaluate growth. To evaluate basic wood density and pulp yield, as well as the genetic and phenotypic associations between the three traits, data of 300 open-pollinated progenies representing 30 selected families from 11 provenances were used.

Narrow-sense heritabilities for all three traits were estimated from data collected in a single *E. urophylla* provenance/progeny trial planted in northern KwaZulu-Natal. The results showed that significant provenance effects for growth, basic wood density and pulp yield were observed. Heritability was found to be strong for basic wood density (h^2 = 0.51) and moderate to weak for volume growth and pulp yield (h^2 = 0.17 and h^2 = 0.11, respectively). This suggests that big genetic gains can be achieved for basic wood density. Although the heritability estimates for volume growth and pulp yield were

weaker, this still allows for tree breeders to make significant genetic gains through accurate selection from this *E. urophylla* breeding population.

Genetic and phenotypic associations between the three traits were estimated from data collected in the same trial. The genetic correlation between volume growth and pulp yield was positive and moderately strong (r_A = 0.66). The genetic correlation estimate between volume growth and basic wood density was found to be negative but weak (r_A = -0.08). The genetic association between pulp yield and basic wood density was found to be positive but weak (r_A = 0.17). Correlation estimates between volume growth and basic wood density, as well as between pulp yield and basic wood density produced standard errors greater than the correlation itself (s.e. = ± 0.32 and ± 0.22, respectively). These high standard errors, coupled with weak genetic correlations, suggest that these correlation estimates are non-significant, but are probably a result of utilizing a small sample size. However, these correlations have a value in making breeding choices, if treated with caution.

Key words: *Eucalyptus urophylla*, provenance, growth, basic wood density, pulp yield, heritability, genetic correlation

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CHAPTER 1. INTRODUCTION

The South African forestry industry, which comprises mainly of exotic plantations, is dynamic and sophisticated. This industry is competing on an aggressive global front, where sustainable, high quality, low cost forest products are in very high demand.

Assessments have shown that the area of the world's natural forests is shrinking. According to estimates (FAO, 2003), a total of 9.4 million hectares of the world's natural forests were converted to other land uses (i.e. deforested) each year, for the period 1990-2000. The annual change in natural forest area by geographical region between 1990 and 2000 is shown in Figure 1.1.

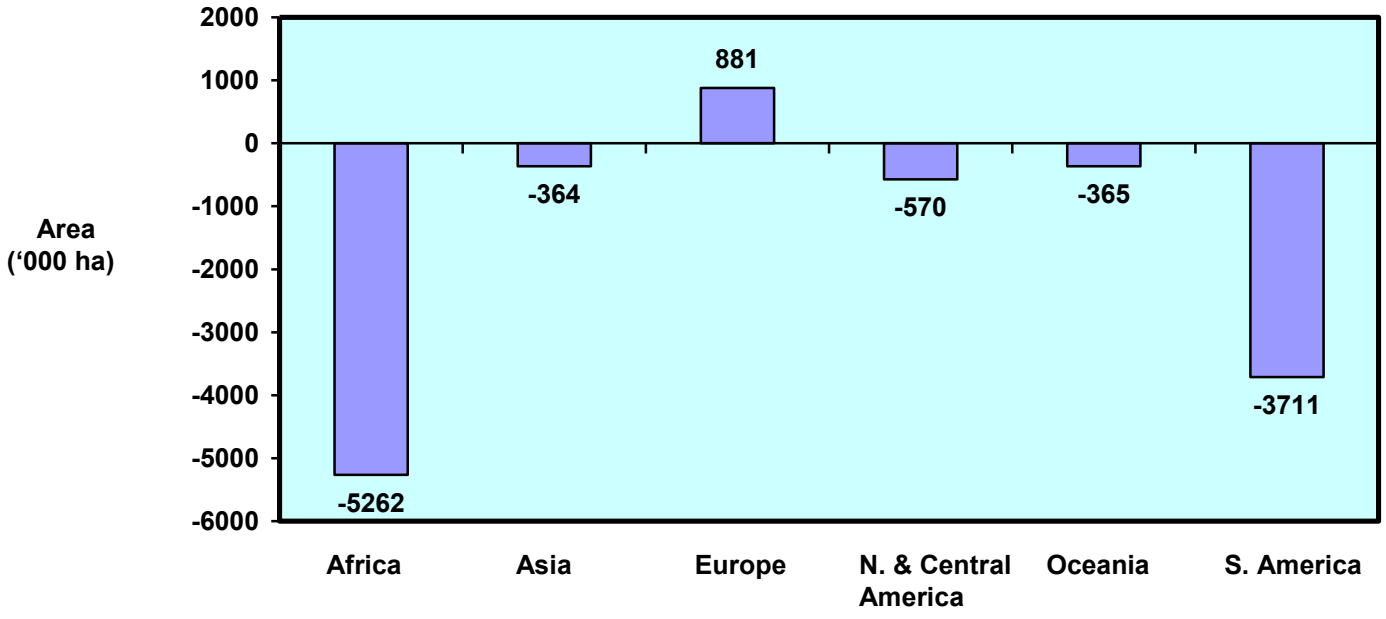

Figure 1.1. Annual changes in natural forest area by main geographical regions between 1990 and 2000 (FAO, 2003)

This reduction in the world's natural forests, coupled with large human population increases and growing per capita consumption is placing unprecedented strains on resources, and presents continued challenges to the sustainable management of the world's natural forests. However, plantation forests have the potential to meet increased demand for industrial wood products and thus their indirect role in conserving natural forest resources remain an important fact (Brink, 2001).

The area of plantations in the world has been increasing for the past two decades, and this trend is expected to continue. However, in South Africa the rate of forestation started to decrease from 1991 onwards. Unavailability of land, droughts and particularly the obtaining of planting permits under the new water legislation were the most important reasons for the decrease (Louw, 2004). Since 1994 very little expansion in terms of plantation area has taken place. Figure 1.2 indicates the annual new forestation in South Africa for the period 1975 to 2002.

In order to manage increased demand, coupled with a reduction in plantation area, the South African forestry industry is moving away from multiple product development towards a core-business philosophy. The main focus area lies in the international pulp and paper markets and then specifically with growing interest in hardwood *Eucalyptus* pulp and paper. *Eucalyptus* offers several advantages that bring a premium to world pulp and paper markets through economically important traits such as fast volume growth and fiber morphology.

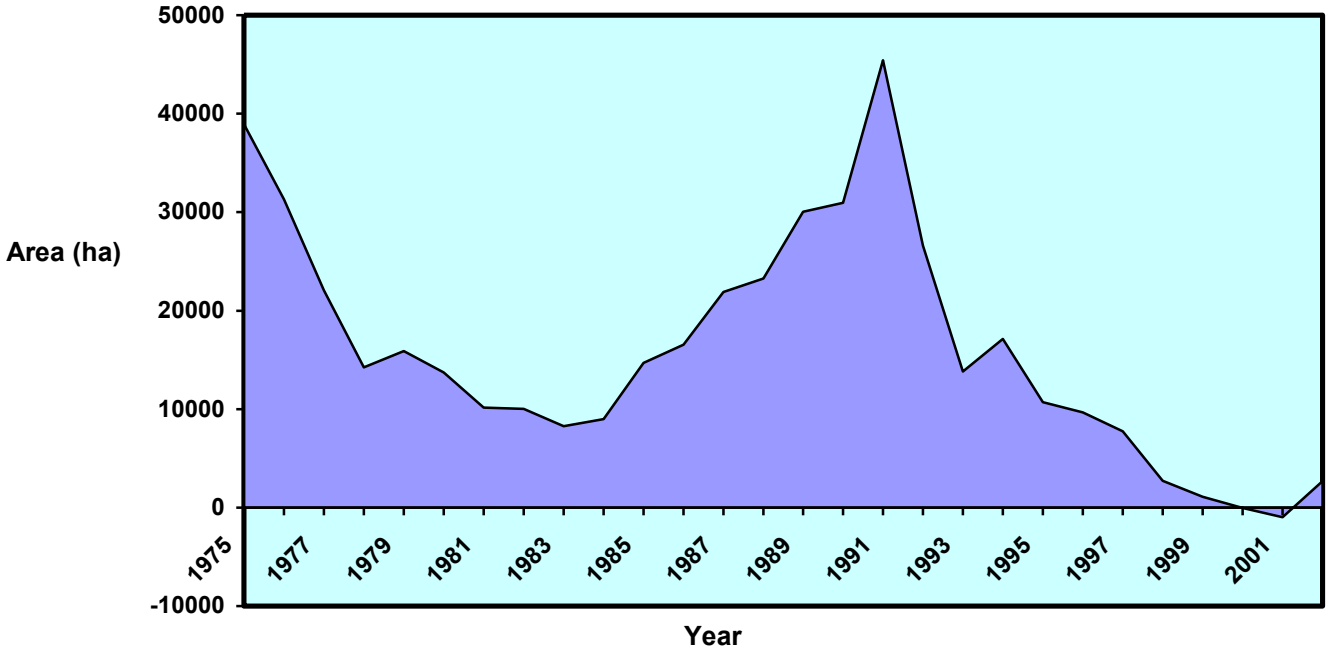

Figure 1.2. Net new additions to South African plantation forests (Godsmark, 2002)

A further development in the South African forestry was the advent of clonal forestry. *Eucalyptus* clonal forestry caught the imagination of prominent South African companies in 1982/83 which resulted from the wide publicity of the Aracruz “Success Story”, and coincided with the rapid expansion of the pulp and paper industry. With the advent of the Mondi plc Kraft pulp mill in Richards Bay, the company decided to convert its land holdings of many thousands of hectares on the Zululand coastal plain to clonal plantations in order to meet future increased demands.

During the late 1980s and early 1990s, in order to satisfy the growing demand for clonal plants, the tendency was to select clones on early performance and good rooting ability, before they could be validated as true winners. With *Eucalyptus grandis* Hill ex Maiden being the species of choice at the time, coupled with severe droughts of 1991 and 1992, the increased incidence of *Eucalyptus* diseases resulted in high mortality rates of *E. grandis* in this region. This had a huge impact on clonal testing strategies as well as choice of species.

During the same period, some positive factors were also observed. *Eucalyptus urophylla* S.T. Blake as well as the hybrid combination *E. grandis* x *E. urophylla* (GU) were found to be more drought tolerant than pure *E. grandis*. In addition to this the GU hybrid also exhibited hybrid vigour that produced growth rates as good as and in some cases even better than *E. grandis*. The GU hybrid also produced a higher basic wood density than *E. grandis*. The importance of *E. urophylla* was fully understood and Mondi took a strategic decision to expand and improve its breeding base for the species.

Although *E. urophylla* has become an important species in the South African forestry industry, there is a lack of reliable genetic information of the species grown in South Africa. This genetic information is required to assist in formulating the efficient operation of a breeding program through which the quality and productivity of plantations may be improved.

The overall aim of this study was therefore to estimate the degree and type of genetic control found within an *E. urophylla* breeding population. Specific objectives of this study were to estimate the components of variation found in the breeding population for certain economically important traits such as growth, basic wood density and pulp yield. From this, the study aimed to determine genetic differences between genotypes for these important traits, as well as estimating genetic parameters such as narrow-sense heritabilities as well as additive genetic correlations between these important traits. This information will be used to formulate the optimum breeding strategy and to predict the likely outcome of selections based on the knowledge of these genetic parameters.

1.1 REFERENCES

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CHAPTER 2. LITERATURE REVIEW

2.1 Introduction

It is estimated that there are over 186 million hectares of forest plantations on a global scale, of which about 116 million are in Asia (including 45 million in China and 33 million in India), 32 million hectares in the European countries (including over 17 million hectares in the Russian Federation), 16 million hectares in the United States, 10.5 million hectares in Japan, 10.4 million hectares in South America (including 5 million hectares in Brazil), 2.8 million hectares in Oceania and 1.5 million hectares in South Africa (FAO, 2003).

An estimated 57% of the plantation area on a global scale is planted with hardwood species and 43% with softwood species. Various species of pines make up the majority (61%) of the softwoods. *Eucalyptus* comprise the largest area of hardwood plantations planted for industrial use (30%), followed by Acacias (12%) and Teak at about 7% (Brink, 2001).

The genus *Eucalyptus* is native to Australia, Indonesia and surrounding islands, and contains a remarkably wide range of tree species with regards to adaptation for different sites, different types of management systems as well as for a variety of uses, both in natural stands and plantations. The *Eucalyptus* genus is one of the most widely propagated tree genera throughout the world. The total area of eucalypt plantations in the world may well have exceeded 6 million hectares by 1985. However, it must be

emphasized that statistical information on plantation areas from many countries is incomplete and that the figure of 6 million hectares must be regarded as only a rough approximation. In South Africa, the area planted to eucalypts during 1998 was approximately 598 000 hectares (Owen and Van Der Zel, 2000).

The first advantage of *Eucalyptus* is that it is a fast growing, highly adaptable genus. Fast growth and good survival lead to short rotations, which in forestry terms is a good return on investment. In saying this, one always has to keep in mind that wood prices and costs such as silviculture, harvesting and transport will always have an important impact on what a forestry company's Internal Rate of Return will be. An added dimension of fast growth and thereby short rotations, if utilized properly, is quick results from genetic improvement of commercial crops. This alone gives *Eucalyptus* grown in certain areas of the Southern hemisphere a distinct advantage over hardwood species grown in the Northern hemisphere. Over the same period, *Eucalyptus* can produce five to ten times as much wood as North Carolina's state forests, where forest species such as *Pinus taeda* L., *Pinus elliottii* Engelm. and *Pinus virginiana* Mill. are grown. This makes foreign wood much cheaper (Kellison, 2001).

In countries such as Argentina, Australia, Brazil, Indonesia, Portugal, Spain and South Africa, pulp and paper companies consistently harvest trees within an age class range of seven to ten years. Figure 2.1 indicates the respective *Eucalyptus* plantation growth rates for the countries mentioned above.

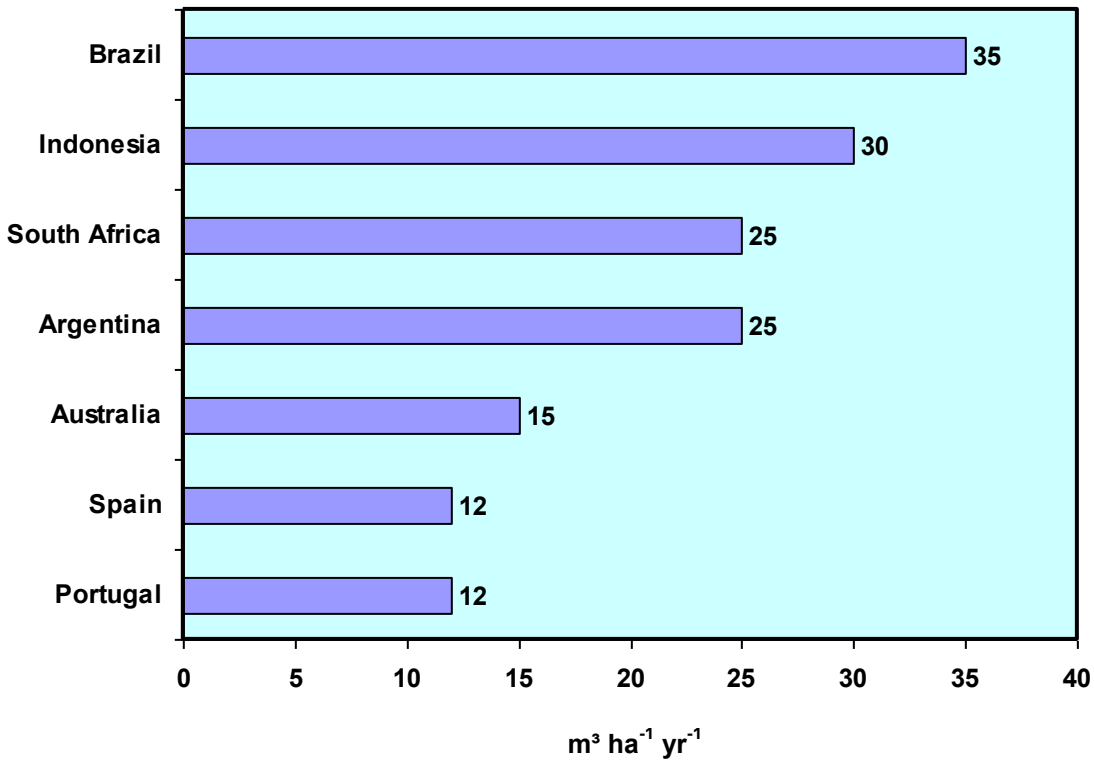

Figure 2.1. Eucalyptus plantation growth rates for various countries

The second advantage that *Eucalyptus* has is its very special fiber morphology that lends itself to high value pulp and paper products. The purpose of pulp making is to separate fibers from each other. These fibers can then be put together again on the paper machine, in the form of a sheet whose properties and basis weight are designed for a specific end use. Delignification and separation of eucalypt wood fibers and bleaching can be achieved with a high pulp yield and low consumption of chemicals (Valente *et al*. 1992). This makes wood fibers of *Eucalyptus* a highly productive and cost effective raw material for the production of pulp for the paper making industry.

2.2 Importance of *Eucalyptus urophylla* S.T. Blake

In the last decade or two, *E. urophylla* has become increasingly important for wood production in plantations at low altitude, seasonally dry tropics to subtropics. It may be successfully grown as a pure species, or as a hybrid with *Eucalyptus grandis* Hill ex Maiden, at low altitudes where few other *Eucalyptus* species grow successfully (Gunn *et al.* 1995). Its success arose from outstanding performance in the Congo and Brazil where it proved to be much more resistant to disease than *E. grandis* while still growing well. Resistance to drought and plantation diseases are the two main reasons why *E. urophylla* has become an important species in South Africa.

Eucalyptus urophylla is one of only two species that are not indigenous to Australia (Gunn *et al.* 1995); the other is *Eucalyptus deglupta* Blume. The known natural occurrence of *E. urophylla* is restricted to seven islands of the lesser Sunda Archipelago, Indonesia: Flores, Adonara, Lembata, Pantar, Alor, Wetar and Timor. The species grows extensively on Alor, Wetar and Timor but is less common on the other islands. On Timor it is known as Ampupu and on Flores it is called Popoo. Latitudinal range is 7°30'-10°00' south, with longitudinal range 122°00'-127°00 east. It occurs predominantly between 300 and 1100m above sea level, although smaller groups of trees grow at altitudes as high as 3000m above sea level. On drier sites it often grows in association with *Eucalyptus alba* Reinw. ex Blume.

Eucalyptus urophylla belongs to the subgenus *Symphyomyrtus* which consist of species with two operculums. Further taxonomic subdivision allows us to divide the subgenus

into sections. *Eucalyptus urophylla* falls into the section *Transversaria*, which also contains *E. grandis*, allowing for hybridization between species. The importance of this lies in the fact that hybrid non-viability tends to increase with increasing distance between taxa, and to create a successful hybrid program between species, one needs to keep the taxonomic evolution between species in mind (Potts and Dungey, 2004).

Up until the late 1970s, *E. urophylla* was a relatively unknown species in South Africa, with few people in the industry recognizing its high economic potential. During 1973 and 1974 the first three trials containing substantial numbers of *E. urophylla* and *E. alba* seed lots were established in South Africa. One trial was established in the semi-temperate eastern province of Mpumalanga, with the other two trials established in subtropical Zululand. *Eucalyptus grandis* was planted as a control across all three trials. From seven year trial results, it was shown that *E. urophylla* outperformed *E. alba* in all traits measured. These traits include survival, stem form, volume growth and basic wood density. However, the true test for *E. urophylla* lay in its performance against the well known and preferred *E. grandis*. Although *E. urophylla's* survival was generally very good, it did show a distinct frost sensitivity, more so than *E. grandis*. For stem form *E. urophylla* performed well although it did not outperform *E. grandis* in this regard (Darrow and Roeder, 1983).

Wood samples taken from *E. urophylla* in these trials to do basic wood density tests have shown some very interesting trends. For wood samples taken at the age of 50 months at Kwambonambi in Zululand, the *E. urophylla* seed lots had a mean basic

density of 446.9kg.$(m^3)^{-1}$, while *E. grandis* of the same age had a mean basic density of 340.9kg.$(m^3)^{-1}$. This gave *E. urophylla* a 31.1% greater density than *E. grandis*. At Frankfort in Mpumalanga, the margin was even greater with *E. urophylla* having a 32.3% greater density than *E. grandis* (Darrow and Roeder, 1983). These results indicated that *E. urophylla* is a good general purpose timber and also has the potential to become a preferred pulp species.

Strangely, these exciting results did not draw a significant reaction from South African forestry industry at the time. Attempts to ensure a more comprehensive series of provenances of *E. urophylla* for testing in all the subtropical regions in the country did not happen immediately. It would take almost another decade before interest in the species was revived. The main reason for the slow reaction was that of the performance of *E. urophylla* for volume production when compared to *E. grandis*. Volume production per hectare is based on the estimates of mean tree volume per plot, multiplied by the stocking of that plot, expressed as stems per hectare. Estimates of the mean annual increment (MAI) are derived by dividing the estimates of volume production per hectare by the age of the trees at time of measurement. The MAI for *E. urophylla* at Frankfort was 24.7$m^3.ha^{-1}.yr^{-1}$ whilst *E. grandis* had an MAI of 37.9$m^3.ha^{-1}.yr^{-1}$. This gave *E. grandis* a 53.6% greater volume production over *E. urophylla*. At Kwambonambi the MAI for *E. urophylla* was 19.7$m^3.ha^{-1}.yr^{-1}$ whilst *E. grandis* produced an MAI of 32.2$m^3.ha^{-1}.yr^{-1}$. Here it gave *E. grandis* a 63.1% greater volume production over *E. urophylla*.

This significant volume growth advantage that *E. grandis* had over *E. urophylla*, as well as taking into consideration that during the early 1980s the single most important driver for plantation forestry was volume growth, the industry did not see the need to increase the genetic base of *E. urophylla* dramatically. Due to this there was no need to study the silviculture or genetic components of this species. In addition, *Eucalyptus* hybrid clonal forestry only came to the fore during the mid 1980s, hence *E. grandis* remained the species of choice until then.

2.3 Quantitative studies of economically important traits: Patterns and magnitude of genetic variation found between different genotypes

It is known that genetic and site factors affect tree growth. Growth should therefore be an important selection criterion for maximizing production (Miranda and Pereira, 2002). It is also of economic importance to select for wood properties that have a major impact on pulp and paper properties (Raymond and Schimleck, 2002). Studies have identified basic wood density and pulp yield as key variables in the profitability of eucalypt Kraft pulp production (Dean *et al*. 1990; Borralho *et al*. 1993; Greaves *et al*. 1997). These wood properties, together with growth, exhibit continuous variation and are viewed as quantitative traits influenced by multiple genetic factors and the environment (Raymond, 2002).

Prior to the mid 1990s, most quantitative studies on eucalypts for pulp production focused on growth, with the important wood traits largely ignored. For assessing genetic effects on wood quality, large numbers of wood samples need to be processed (Raymond and Schimleck, 2002). Traditional wood density screening and, pulping methods in particular, are too slow and costly to allow for screening of large numbers on a regular basis (Raymond and Schimleck, 2002).

An alternative to traditional pulping is to use a secondary standard, such as cellulose content of the wood, which has been shown to be strongly correlated with Kraft pulp yield (Wallis *et al*. 1996a, 1996b; Kube and Raymond, 2002). There is an excellent agreement between pulp yield and predicted cellulose content (Raymond and

Schimleck, 2002). As with pulp yield screening, the screening of basic wood density has undergone improvements that has allowed for large sample sizes to be processed in a quick and relatively cheap manner. Basic density is now commonly assessed using a core taken near breast height, which has been shown to be highly correlated to whole tree values (Lausberg *et al*. 1995; Raymond and Muneri, 2001; Kube and Raymond, 2002). Basic wood density has also been assessed using a Pilodyn, which is an instrument that drives a flat-nosed pin into a wood sample with a known force. The depth of penetration is negatively correlated with basic density (Greaves *et al*. 1996; Raymond and MacDonald, 1998; Raymond *et al*. 1998). Some studies have found that Pilodyn precision to be low and unreliable for selecting individual trees (Raymond *et al*. 1998). However, the low cost, speed and simplicity of this method remain strong advantages and, for this reason, it is still being used (Kube and Raymond, 2002).

In order to improve the productivity of plantation forests, tree breeding programs exploit genetically variable populations to develop superior trees. A basic knowledge of the genetic characteristics of the population is necessary to conduct effective breeding and selection. Quantitative information is required about the various components that contribute to total variation, the size of genetic variances, the type of gene action, and the heritability and genetic correlations for economically important traits. This enables the outcome of selection, particularly genetic gains, to be predicted. It also helps to determine likely difficulties in selection and the strategies to overcome such problems. In a wider context, it broadens knowledge of the genetics and breeding behaviour of the species involved (Eismann *et al.* 1990).

Despite the extensive use of various eucalypts around the world in plantation forestry, estimates of genetic parameters for economically important traits in *Eucalyptus* species in general are not abundant in the literature (Volker *et al*. 1990; Hodge *et al*. 1996). In saying this, the review did produce some results on genetic trends of economically important traits. This gives the opportunity for comparisons and conclusions to be made regarding these traits of eucalypts.

From the literature review on traits such as growth, wood density and pulp yield, it became clear that a wide range of genetic experiments can be deployed to answer one or more of a range of genetic questions. Regardless of the purposes for designing and implementing genetic tests, accurate analysis and interpretation of data are always needed if precise and accurate sources of variation and genetic parameters are to be estimated. This is crucial for making sound decisions in many stages of a tree improvement program (Hodge and White, 1986). It has long been recognized that efficient advanced-generation improvement relies upon accurate estimates of heritability and genetic correlations. Knowledge of these genetic parameters enables selection responses to be predicted and breeding strategies to be evaluated. Reliable parameter estimates also facilitate the development of optimal selection indices and the best linear prediction of breeding values (Cotterill and Dean, 1990).

A popular technique deployed in *Eucalyptus* genetic tests is to group families from the same provenance together (e.g., Emery and Ledig, 1987; Burgess, 1988; Otegbeye, 1991; Chamshama *et al*. 1999; Jianzhong, 2003; Tibbits and Hodge, 2003; Ginwal *et al*.

2004). A provenance is defined as: "*The original geographic area from which seed or other propagules were obtained*" (Zobel and Talbert, 1984). By doing this, an extra genetic component can be added to the analysis of variance, thereby helping to distinguish more accurately which proportion of the total phenotypic variance is due to genetics and which proportion is due to the environment.

Another important observation made during the literature review is to treat the estimated genetic components with caution. The use of wrong genetic parameters is known to result in biased estimates of breeding values (White and Hodge, 1990). Often genetic parameter estimates are made using small experiments which contain a limited number of genetic treatments. In a study done by Tibbits and Hodge (2003), they found that the significance of provenance effects altered upon reducing the number of provenances from the dataset. In a study done to determine the genetic parameters for *Eucalyptus globulus* Labill., it was found that the relatively high error variances of the estimates based on progeny data was due to the small number of families represented (Araujo *et al*. 1996). In some cases, for example, in the data presented by Cotterill and Dean (1988), the changes reported in additive variance over time were associated to varying degrees with different thinning regimes (i.e., stocking density) and were not genetic effects *per se*. In a study done on *E. urophylla*, high mortality rates made it possible for certain trees to grow more upon having more space, and therefore increased the environmental variability. This resulted in very low heritability estimates (Sanches-Vargas *et al*. 2004).

If variance components are estimated on a single-site basis then family-by-environment interaction variance cannot be estimated, and in fact this component of variance is added to the estimate of family variance on that site. Thus, estimates of variance among families include both family and family-by-environment variance. The result of this is that heritability estimates are inflated and therefore known as biased heritability estimates (Comstock and Moll, 1963).

A primary reason for designing and implementing genetic tests is the ability to determine the patterns and magnitude of genetic variation found between different genotypes in a breeding population. This assists in identifying superior genotypes for the use in forestation programs.

Results from studies done to determine patterns and magnitude of genetic variation, as well as significance of genetic components and heritability estimates for growth and wood traits across various *Eucalyptus* species are presented in Table 2.1.

From the results presented in Table 2.1, it seems that if a trait is under strong genetic control, as compared to a trait under weak genetic control, it becomes easier to distinguish between the different genotypes, thereby making it possible to identify superior genotypes for future breeding and commercial deployment strategies. Another way of explaining this is that if the proportion of additive genetic variance becomes a significant proportion of the total phenotypic variance, hence a higher heritability, the differences between genotypes become more apparent, thus making the selection

process for superior genotypes more effective. Another interesting observation made from the results in Table 2.1 is that heritabilities for wood properties are higher than those for growth properties, which are under moderate to strong genetic control. This provides the opportunity for tree breeders to achieve significant genetic gains for growth, and even more so for wood density and pulp yield, thereby improving the yields derived from commercial plantation crops.

Table 2.1. Results from studies done to determine significance of genetic components and heritability estimates for growth and wood traits across various *Eucalyptus* species.

Eucalyptus Species	**Trait** [a]	**Age (months)**	**Component of variance** [b]	**Level of significance based on F-statistic** [c]	h^2/H^2	**Author**
cloeziana	DBH	67	σ^2_F	**	0.31	Marques *et al*. 1996
globulus	BA	72	σ^2_F	**	0.15	Borralho *et al*. 1992
	WD	60	σ^2_F	**	0.33	MacDonald *et al*. 1997
	DBH	96	σ^2_P	ns	0.06	Muneri and Raymond, 2000
	WD	96	σ^2_P	**	0.63	
	PY	96	σ^2_P	**	0.41	Raymond *et al*. 2001
	WD	48	σ^2_F	ns	0.11	Silva *et al*. 2004
	DBH	132	σ^2_P	**	0.20	Apiolaza *et al*. 2005
	WD	132	σ^2_P	**	0.44	
	CC	132	σ^2_P	**	0.84	
	PY	132	σ^2_P	**	0.43	
grandis	WD	72	σ^2_C	**	0.36	Osorio *et al*. 2001
nitens	DBH	72	σ^2_P	ns	0.11	Gea *et al*. 1997
	WD	72	σ^2_P	**	0.45	

Table 2.1 continued

Eucalyptus species	Trait [a]	Age (months)	Component of variance [b]	Level of significance based on F-statistic [c]	h^2/H^2	Author
nitens	BA	48-96	σ^2_P	**	0.19	Tibbits and Hodge, 1998
	WD	48-96	σ^2_P	**	0.42	
	PY	48-96	σ^2_P	**	0.37	
	DBH	144	σ^2_F	---	0.39	Kube *et al*. 2001
	WD	144	σ^2_F	---	0.51	
	CC	144	σ^2_F	---	0.54	
	BA	91	σ^2_P	ns	0.10	Tibbits and Hodge, 2003
obliqua	DBH	156	σ^2_F	**	0.57	Matheson *et al*. 1986
	WD	156	σ^2_F	**	0.84	
	PY	156	σ^2_F	**	0.48	
pellita	DBH	72	σ^2_F	**	0.25	Leksono *et al*. 2006
regnans	DBH	45	σ^2_F	**	0.46	Griffin and Cotterill, 1988
	HT	45	σ^2_F	**	0.43	
	VOL	45	σ^2_F	**	0.45	
tereticornis	DBH	72	σ^2_P	**	0.73	Otegbeye, 1991
	HT	21	σ^2_P	**	0.29	Ginwal *et al*. 2004
urophylla	DBH	84	σ^2_F	ns	0.01	Mori *et al*. 1990
	HT	84	σ^2_F	**	0.19	
	VOL	84	σ^2_F	ns	0.05	
	WD	48	σ^2_F	**	0.76	Brasil and Veiga, 1994
	WD	72	σ^2_P	**	0.71	Wei and Borralho, 1997
	WD	84	σ^2_F	**	0.60	Jianzhong, 2003
	DBH	72	σ^2_P	ns	0.10	
	VOL	72	σ^2_P	ns	0.07	

a) DBH = diameter at breast height; WD = wood density; CC = cellulose content; PY = pulp yield; BA = basal area; HT = height; VOL = volume

b) σ^2_F = variance due to family; σ^2_P = variance due to provenance; σ^2_C = variance due to clone

c) Significant levels are ns ($P > 0.05$), ** ($P < 0.01$)

2.4 Quantitative studies of economically important traits: Age-associated changes in genetic control of traits

Determining age-associated changes in genetic control of important traits, and the implications it may have for early selection, is another important reason why genetic experiments are implemented. Shortening the generation intervals in forest tree breeding is essential to maximize genetic gains per unit time (Cotterill, 1985). Therefore, tree breeders need to know the earliest age at which trees can be measured in order to predict their ultimate rotation age performance.

The majority of economically important traits in forestry breeding for pulp wood, such as growth, wood density and pulp yield, are controlled by many loci. The tree breeder has to increase the frequency of favorable alleles in the loci to improve the phenotypic expression of these traits. In order to accumulate the favorable alleles underlying additive genes, repeated cycles of selection, named recurrent selection, must be carried out (Hallauer, 1992).

The use of recurrent selection in forestry breeding, such as in the case of eucalypts, is limited mainly because of the length of each cycle. An alternative is to carry out early selection, assessing progenies or individuals at the youngest possible stage (Marques *et al*. 1996). Development of techniques to select at very young ages for performance at rotation age would greatly reduce generation intervals, increasing genetic gain per unit time, and thus, substantially accelerate tree improvement efforts (Lambeth, 1980).

Information on age-age correlations for important traits of short-rotation species such as eucalypts has mostly been generated since the late 1980s, and then mainly focusing on growth traits (Borralho *et al*. 1992; Marques *et al*. 1996; Greaves *et al*. 1997; Wei and Borralho, 1998; Jianzhong, 2003; Osorio *et al*. 2003; Ignacio-Sanchez *et al*. 2005). In many studies, there is little information available about patterns of change of wood properties with increasing age (Raymond, 2002).

Efficiency of early-age selection is a function of the heritabilities of the trait at different ages, coupled with the additive genetic correlation between different ages for the same trait (Osorio *et al*. 2003). To ensure efficient early-age selection, the tree breeder therefore needs to know if the magnitude of additive genetic and phenotypic variances changes over time. It is also important to know if the ratios of these two components (i.e., heritabilities) also change over time (Kang, 1985).

Although few results are available for growth and wood traits, it is clear from the forestry literature that the magnitude of additive genetic and phenotypic correlations, together with heritabilities of these traits, changes over time. Table 2.2 and Table 2.3 present results from studies that examined the age-associated changes of additive genetic and phenotypic correlations, as well as the changes in heritabilities over time, respectively.

Where more than one age class per trait were investigated, it seems that additive genetic correlations between mature and juvenile measurements decreased as pairs of measurements became further apart in time (Borralho *et al*. 1992; Marques *et al*. 1996;

Greaves *et al*. 1997; Wei and Borralho, 1998; Jianzhong, 2003; Osorio *et al*. 2003). It would therefore be important for the tree breeder to establish at which earlier-age tree measurements could be used to efficiently predict outcomes at harvesting age.

Evaluations of growth traits showed that measurements made in the first two years after planting provided a poor estimate of subsequent growth (Van Wyk, 1976; Borralho *et al*. 1992; Marques *et al*. 1996; Wei and Borralho, 1998; Jianzhong, 2003; Osorio *et al*. 2003; Ignacio-Sanchez *et al*. 2005). Kang (1985), also concluded that selection ages of less than one third of the rotation age should be used with caution. Griffin and Cotterill (1988), also noted that even for such fast growing trees as *Eucalyptus*, it takes at least one growing season to overcome maternal and nursery effects. Zobel and Talbert (1984), noted that taking measurements of trees at half the rotation age is common for final assessment of families and individuals. Another consideration that should be taken note of when deciding on the best early-age assessment, is that although optimum age for selection is determined in terms of genetic gain per unit time, it should be considered in relation to the age at which the species becomes sexually mature and produces seed (Gwaze *et al*. 1997). A tree breeder may therefore make early-age predictions that will give an accurate indication of rotation-age performance, yet will have to wait for the trees to flower before seed may be collected to construct the next breeding generation.

Although results on wood traits are very limited, it seems that at least for wood density, there is a much stronger relationship between early and late measurements than with growth traits (Greaves *et al*. 1997; Osorio *et al*. 2003).

Growth and wood density traits show increasing individual heritabilities with increasing age, a trend commonly found in short rotation eucalypts (Van Wyk, 1976; Otegbeye, 1991; Borralho *et al*. 1992; Greaves *et al*. 1997; Jianzhong, 2003; Osorio *et al*. 2003; Ignacio-Sanchez *et al*. 2005; Leksono *et al*. 2006). These results suggest that early age selection of the parents may not be beneficial, and that selection would be more efficient when older trees are used in the selection process. However, in a study done by Marques *et al*. (1996), where the trends in heritability for diameter growth of *Eucalyptus cloeziana* F. Muell. were investigated, they found that heritabilities decreased steadily over the first five years of growth after which it stabilized and remained relatively constant until the last assessment at age seven years. These results suggest that the earlier selections are made, the greater the genetic gains will be. In a study by Wei and Borralho (1998), where changes in heritability for height growth of *E. urophylla* were investigated, they found that heritabilities increased marginally over the first three years of growth after which it reached a relatively stable value until plantation rotation age. This study suggested that the best time for early-age selections would be at three years.

Overall, studies on age-trends of heritabilities show divergent trends in heritability over time. For early-age selection (optimum age for selection), the results from different studies vary widely, and their general applicability is constrained by differences in species, sample size, time intervals considered, test environment, trial design and silviculture treatments applied (Wu, 1999).

A further observation made on results where age-trends of heritabilities were investigated, is that the trend must be looked at in conjunction with the magnitude of variation that falls under genetic control. Although heritabilities for growth and wood traits generally increase with increased age, different species in different environments express various levels of genetic control. In a study done by Jianzhong (2003), where age-trends in heritabilities for diameter growth and wood density were investigated, he found that, although heritabilities for both traits showed an increase with increased age, the magnitude of genetic control over both traits were quite different and therefore they had different results for early-age selection. For diameter growth the heritabilities were very low. This lead to a situation where significant differences between provenances did not develop until the age of five years and differences between families only developed at the age of six years. For wood density the genetic control was very strong, to such an extent that significant differences between treatments were observed from a very early age. Nearly half of the total phenotypic variation observed at the age of five years was due to genetic influence. Thus, for this study it would be possible to select at an earlier age for wood density but selections for diameter growth would need to wait until trees were aged five to six years. Greaves *et al*. (1997), found similar strong heritabilities for wood density in a study done on *Eucalyptus nitens* Deane & Maiden.

Table 2.2. Inter-age additive genetic and phenotypic correlations of important traits of some *Eucalyptus* species.

Eucalyptus species	**Juvenile trait** [a]	**Mature trait** [a]	**Additive genetic correlation (r_A)**	**Phenotypic correlation (r_P)**	**Author**
camaldulensis	HT 18	HT 66	---	0.59	Emery and Ledig, 1987
cloeziana	DBH 29	DBH 80	0.88	---	Marques *et al*. 1995
	DBH 42	DBH 80	0.94	---	
	DBH 56	DBH 80	0.96	---	
	DBH 67	DBH 80	0.98	---	
globulus	HT 12	HT 48	0.56	0.62	Borralho *et al*. 1992
	HT 24	HT 48	0.90	0.88	
grandis	HT 06	HT 15	0.52	0.79	Van Wyk, 1976
	DBH 06	DBH 15	0.21	0.72	
	VOL 06	VOL 15	0.37	0.69	
	MAI 24	MAI 72	0.44	---	Osorio *et al*. 2003
	MAI 36	MAI 72	0.84	---	
	MAI 48	MAI 72	0.96	---	
	MAI 60	MAI 72	0.99	---	
	HT 36	HT 72	0.77	---	
	WD 36	WD 72	0.95	---	
nitens	WD 36	WD 84	0.93	---	Greaves *et al*. 1997
	WD 48	WD 84	0.98	---	
	WD 60	WD 84	1.00	---	
	WD 72	WD 84	1.00	---	
	DBH 72	DBH 144	0.79	0.79	Kube *et al*. 2001

Table 2.2 continued

Eucalyptus species	Juvenile trait [a]	Mature trait [a]	Additive genetic correlation (r_A)	Phenotypic correlation (r_P)	Author
urophylla	DBH 12	DBH 60	0.70	0.68	Wei and Borralho, 1998
	DBH 24	DBH 60	0.98	0.85	
	DBH 36	DBH 60	0.99	0.91	
	DBH 48	DBH 60	1.00	0.96	
	HT 12	HT 60	0.78	0.66	
	HT 24	HT 60	0.95	0.85	
	HT 36	HT 60	1.00	0.91	
	HT 48	HT 60	0.99	0.96	
	DBH 36	DBH 48	0.86	---	Jianzhong, 2003
	DBH 36	DBH 60	0.79	---	
	DBH 36	DBH 72	0.73	---	
	DBH 36	DBH 84	0.66	---	
	WD 36	WD 48	0.82	---	
	WD 36	WD 60	0.81	---	
	WD 36	WD 72	0.70	---	
	VOL 12	VOL 36	0.79	---	Ignacio-Sanchez *et al*. 2005
	VOL 24	VOL 36	0.97	---	

a) Number after trait abbreviation is age indicated in months

Table 2.3. Inter-age changes in heritability of important traits of some *Eucalyptus* species.

Eucalyptus species	**Trait** [a]	**Heritability**	**Author**
cloeziana	DBH 29	0.41	Marques *et al*. 1996
	DBH 42	0.36	
	DBH 56	0.31	
	DBH 67	0.31	
	DBH 80	0.34	
globulus	HT 12	0.21	Borralho *et al*. 1992
	HT 24	0.20	
	HT 48	0.29	
	HT 72	0.34	
	HT 96	0.35	
grandis	HT 06	0.10	Van Wyk, 1976
	HT 15	0.11	
	DBH 06	0.05	
	DBH 15	0.08	
	VOL 06	0.06	
	VOL 15	0.10	
	MAI 24	0.14	Osorio *et al*. 2003
	MAI 36	0.14	
	MAI 48	0.17	
	MAI 60	0.20	
	MAI 72	0.22	
nitens	DBH 48	0.37	Greaves *et al*. 1997
	DBH 84	0.42	
	WD 36	0.31	
	WD 48	0.43	
	WD 60	0.49	

Table 2.3 continued

Eucalyptus species	Trait [a]	Heritability	Author
nitens	WD 72	0.53	Greaves *et al*. 1997
	WD 84	0.53	
	DBH 72	0.17	Kube *et al*. 2001
	DBH 144	0.39	
pellita	DBH 12	0.17	Leksono *et al*. 2006
	DBH 24	0.15	
	DBH 36	0.22	
	DBH 48	0.24	
	DBH 72	0.25	
tereticornis	DBH 36	0.51	Otegbeye, 1991
	DBH 60	0.52	
	DBH 72	0.73	
urophylla	HT 12	0.17	Wei and Borralho, 1998
	HT 24	0.20	
	HT 36	0.23	
	HT 48	0.23	
	HT 60	0.24	
	DBH 12	0.13	
	DBH 24	0.14	
	DBH 36	0.18	
	DBH 48	0.20	
	DBH 60	0.23	
	DBH 36	0.00	Jianzhong, 2003
	DBH 48	0.00	
	DBH 60	0.01	
	DBH 72	0.07	
	DBH 84	0.10	
	VOL 36	0.01	

Table 2.3 continued

Eucalyptus Species	Trait [a]	Heritability	Author
urophylla	VOL 48	0.03	Jianzhong, 2003
	VOL 60	0.13	
	VOL 72	0.08	
	VOL 84	0.15	
	WD 36	0.34	
	WD 48	0.43	
	WD 60	0.47	
	WD 72	0.60	
	HT 12	0.34	Ignacio-Sanchez *et al*. 2005
	HT 24	0.43	
	HT 36	0.49	
	DBH 12	0.25	
	DBH 24	0.44	
	DBH 36	0.49	
	VOL 12	0.26	
	VOL 24	0.44	
	VOL 36	0.52	
	WD 36	0.69	

a) Number after trait abbreviation is age indicated in months

2.5 Quantitative studies of economically important traits: Trait-trait correlations

Another major reason for implementing genetic experiments is to determine trait correlations and the implications these may have on the selection process. It is important for tree breeders to know what the genetic association between different traits of importance is. The genetic correlation (r_A) between two economically important traits is of particular importance since efficient selection for quality and production relies strongly on both traits.

During the process of selecting improved genotypes for advanced breeding and commercial deployment, tree breeders need to take into consideration whether a positive or negative association exists between different important traits. A positive association between two traits means that tree breeders only have to measure one of the traits (usually the trait that is easy and cost effective to measure), make selections based on data from the measured trait only, and still achieve a positive outcome for the other trait. On the other hand, if a negative association exists, such a selection process will result in the genetic erosion of the second, non-measured trait. In such a case of negative genetic association, data from both traits will have to be utilized to develop selection indices (White and Hodge, 1989; Cotterill and Dean, 1990). Both traits are taken into consideration according to their individual weight of importance towards overall economic performance. This will result in a single selection index value that is then used in the process of selecting improved genotypes. Results from various studies that examined the genetic and phenotypic association between different traits of economic importance for some *Eucalyptus* species are presented in Table 2.4.

One important issue when designing a plantation tree breeding strategy is the relationship between tree growth rate and wood quality (Raymond, 2002). Improving both productivity and product quality of plantations is the goal of forestry research, and tree breeding in particular (Kube *et al*. 2001). Historically, improving productivity (growth) has been the main priority. It has not been until recently that wood properties (quality) have become an integral part of *Eucalyptus* breeding programs (Gea *et al*. 1997; Tibbits and Hodge, 1998). Wood properties are now widely recognized as important to end-product value and overall profitability. Studies have found that increased wood density (WD) and pulp yield (PY) to be of economic importance (Dean *et al*. 1990; Borralho *et al*. 1993; Greaves *et al*.,1997).

For assessing the quality of a plantation resource, or evaluating silvicultural or genetic effects on wood quality, large numbers of samples need to be processed (Raymond and Schimleck, 2002). Traditional pulping methods are limited because they are destructive (sample trees need to be felled), time consuming and expensive (Downes *et al*. 1997; Raymond and Schimleck, 2002), and do not allow for the screening of such large numbers on a regular basis. An alternative method is to use a secondary standard, such as the cellulose content (CC) of the wood, which has been shown to be strongly correlated with Kraft pulp yield (Wallis, 1996a, 1996b; Kube and Raymond, 2002).

There is a strong and positive genetic correlation between pulp yield and cellulose content. This was shown in studies done by Raymond and Schimleck (2002), Thamarus *et al*. (2004) and Apiolaza *et al*. (2005). The work done by Raymond and Schimleck

(2002), consisted of three separate trials, with all three trials producing correlations between pulp yield and cellulose content above 0.90.

Due to the strong and positive genetic correlation that exists between pulp yield and cellulose content, the correlations between either and wood density is therefore important. Published estimates of genetic correlations between both pulp yield and cellulose content with wood density are highly variable. In a study done on *E. globulus* (Raymond and Schimleck, 2002), the genetic correlations between pulp yield and wood density, as well as between cellulose content and wood density were highly variable. Genetic correlations (r_A) between pulp yield and wood density ranged from zero to strongly positive ($r_A = 0.74$). The correlations between cellulose content and wood density were also variable, ranging between moderately negative ($r_A = -0.33$) and very strongly positive ($r_A = 0.67$). Jianzhong (2003), found that for *E. urophylla*, the correlation between pulp yield and wood density was very strong.

Similar observations were made by Miranda *et al*. (2001). In a study done on *E. globules*, they found that high wood densities are advantageous since they correspond to higher pulp yields on a raw-material volume basis and to a better use of digester capacity in the pulp mill. However, they also stated that too high a wood density may cause difficulties for wood impregnation with the pulping liquor and also, if the high density derives from extensive accumulation of extractives, lower pulp yields and pulp brightness are obtained together with higher chemical consumption and eventual

problems in the recovery process of pulping. Thus, there is a maximum limit to wood density, after which it becomes economically detrimental.

Tibbits and Hodge (1998) investigated the genetic correlation between pulp yield and wood density for an *E. nitens* breeding population. They found that there was a favorable positive relationship between pulp yield and wood density, with a genetic correlation of 0.33. Apiolaza *et al*. (2005), found that the genetic correlation between pulp yield and wood density in an *E. globulus* breeding population was very strong and positive (r_A = 1.08), although they acknowledged that their sample sizes might have been too small to determine an accurate value. They found a similarly strong and positive correlation between cellulose content and wood density (r_A = 0.61).

However, in a study on the same species by Kube *et al*. (2001), they found that there was a negative genetic correlation between cellulose content and wood density (-0.45). They further noted that published estimates of genetic correlations for eucalypts were highly variable and noted that their study was unique in finding strongly negative correlations between these two traits. Similar, but even more negative genetic associations between pulp yield and wood density were found by Wei and Borralho (1997), when they investigated the genetic parameters of an *E. urophylla* breeding population. They reported a genetic correlation of -1.0 between pulp yield and wood density.

There are a number of possible reasons for the variability in estimates of genetic correlations. Firstly, this may be due to the inherent variation between species and populations. Secondly, differences between provenances within a species may also be a source of variation. Thirdly, differences in environments where the trees are grown may also contribute to the variation. Fourthly, some estimates of genetic associations have been made using very small or truncated data sets because wood testing can be relatively costly and this may bias some estimates (Kube *et al*. 2001). Regardless of the reasons for variable genetic correlations, it appears unwise for the tree breeder to assume 'standard' correlations when making selections. A safer approach would be to assess a sample of the population to estimate 'true' genetic correlations and apply these to the estimation of breeding values (Kube *et al*. 2001).

Similar variable results were found in the literature when pulp yield and/or cellulose content were compared to growth traits. Raymond and Schimleck (2002) found within a breeding population of *E. globulus* weak to moderately strong negative associations between diameter growth and pulp yield/cellulose content, with genetic correlations ranging from negative 0.11 to negative 0.51. Apiolaza *et al*. (2005) found for the same species weakly negative (r_A = -0.16) results between diameter growth and pulp yield, but a very strongly positive association between diameter growth and cellulose content (r_A = 0.61). Although the genetic correlations in this study were associated with very large standard errors, the difference between these two groups of correlations does not fit any previously recorded trends. This may be due to the very small sample sizes used in this particular experiment.

Opposite trends were found in studies done on *E. nitens*. Tibbits and Hodge (1998) found a moderately strong and positive genetic correlation between basal area growth and pulp yield (r_A = 0.24). Kube *et al*. (2001) found an even stronger association between diameter growth and cellulose content (r_A = 0.79). Wei and Borralho (1997) found virtually no relationship between height growth and pulp yield in an *E. urophylla* population (r_A = 0.04). They did however find a moderately positive association between diameter growth and pulp yield (r_A = 0.35).

Studies done on the association between growth traits and wood density are relatively abundant. In general, the trends found on genetic correlations between these two traits were more stable. Genetic correlations between growth traits and wood density ranged from zero to strongly negative but never moderately to strongly positive. In a study on *E. globulus*, MacDonald *et al*. (1997) found weakly negative associations between diameter growth and wood density (r_A = -0.25). Raymond and Schimleck (2002) included three independent tests in their analysis, and found genetic correlations between diameter growth and wood density ranged from zero to -0.44. Apiolaza *et al*. (2005), working with the same species, found a stronger negative association between diameter growth and wood density (r_A = -0.58). Osorio *et al*. (2003) investigated *E. grandis* and found genetic correlations between growth and wood density to be virtually zero, ranging from -0.04 to -0.08. Gea *et al*. (1997) found a similar genetic correlation in *E. nitens* (r_A = 0.08). Other studies done on *E. nitens* found genetic correlations between growth and wood density to range from moderately weak and negative (r_A = -0.20), to more strongly negative (r_A = -0.57), (Greaves *et al*. 1997; Tibbits and Hodge, 1998; Kube *et al*.

2001). Wei and Borralho, (1997) found near zero to weakly negative genetic correlations existing between growth and wood density traits in *E .urophylla* (r_A = -0.04 to -0.34). Jianzhong (2003) and Ignacio-Sanchez *et al*. (2005) found similar near-zero genetic correlations between growth and wood density traits for *E. urophylla* (r_A = -0.12 to 0.003).

The practical implications of these genetic correlations between growth and wood density traits are that if the associations are weak, the two traits can be treated as independent traits when carrying out selections. However, for unfavorable negative correlations, improvement on growth traits alone will prejudice wood density. In such cases, selection of superior individuals should include an index value, assigning appropriate weights to wood density and growth, with the exact coefficients dependent on the specific breeding objectives (Borralho *et al*. 1993; Greaves *et al*. 1996).

In all the studies investigated, strong and positive genetic associations were found among the growth traits. These genetic correlations indicate that correlated responses for several growth traits will be obtained if selection is done on only one of them (Van Wyk, 1976). Although all growth traits consistently showed strong and positive genetic correlations amongst each other, the genetic correlations between diameter growth and volume production were substantially higher than those involving height growth and volume production. This reflects the greater contribution of diameter to the estimated conical volume of trees (Griffin and Cotterill, 1988). Height is also a more

difficult and costly trait to measure when compared to diameter growth, especially on trees older than two years (Subramanian *et al*. 1992).

Table 2.4. Additive genetic and phenotypic correlations between economically important traits measured of some *Eucalyptus* species.

Eucalyptus species	**Trait combination** [a]	**Genetic correlation (r_A) (± s.e.)**	**Phenotypic correlation (r_P)**	**Author**
globulus	HT 48 & BA 96	0.93 ± 0.05	0.80	Borralho *et al*. 1992
	HT 96 & BA 96	0.98 ± 0.03	0.86	
	DBH 60 & WD 60	-0.25 ± 0.06	---	MacDonald *et al*. 1997
	DBH 84 & WD 84	0.00 ± 0.21	0.09	[b] Raymond and Schimleck, 2002
	DBH 84 & PY 84	-0.43 ± 0.24	-0.05	
	DBH 84 & CC 84	-0.43 ± 0.25	-0.01	
	WD 84 & PY 84	0.74 ± 0.14	0.19	
	WD 84 & CC 84	0.67 ± 0.17	0.12	
	PY 84 & CC 84	0.97	0.97	
	DBH 96 & WD 96	-0.22 ± 0.34	0.03	
	DBH 96 & PY 96	-0.16 ± 0.35	-0.05	
	DBH 96 & CC 96	-0.11 ± 0.35	0.01	
	WD 96 & PY 96	0.08 ± 0.20	0.15	
	WD 96 & CC 96	0.02 ± 0.20	0.05	
	PY 96 & CC 96	0.96	0.94	
	DBH 96 & WD 96	-0.44 ± 0.25	-0.07	
	DBH 96 & PY 96	-0.43 ± 0.35	-0.12	
	DBH 96 & CC 96	-0.51 ± 0.46	-0.09	
	WD 96 & PY 96	0.00 ± 0.22	-0.20	
	WD 96 & CC 96	-0.33 ± 0.21	-0.28	
	PY 96 & CC 96	0.91	0.97	

Table 2.4 continued

Eucalyptus species	Trait combination [a]	Genetic correlation (r_A) (± s.e.)	Phenotypic correlation (r_P)	Author
globulus	WD 84 & PY 84	---	0.10	Thamarus *et al*. 2004
	WD 84 & CC 84	---	-0.27	
	PY 84 & CC 84	---	0.65	
	DBH 132 & WD 132	-0.58 ± 0.44	---	Apiolaza *et al*. 2005
	DBH 132 & PY 132	-0.16 ± 0.48	---	
	DBH 132 & CC 132	0.61 ± 0.34	---	
	WD 132 & PY 132	1.08 * ± 0.24	---	
	WD 132 & CC 132	0.61 ± 0.25	---	
	PY 132 & CC 132	0.82 ± 0.11	---	
grandis	HT 15 & DBH 15	0.93	0.93	Van Wyk, 1976
	HT 15 & VOL 15	0.94	0.84	
	DBH 15 & VOL 15	0.97	0.90	
	HT 108 & DBH 108	0.56	---	Subramanian *et al*. 1992
	HT 108 & BA 108	0.53	---	
	DBH 108 & BA 108	0.99	---	
	HT 36 & MAI 36	0.80	---	Osorio *et al*. 2003
	HT 36 & WD 36	0.14	---	
	MAI 36 & WD 36	-0.04	---	
	HT 72 & MAI 72	0.87	---	
	HT 72 & WD 72	0.06	---	
	MAI 72 & WD 72	-0.08	---	
nitens	DBH 108 & HT 108	0.92 ± 0.04	0.83	Whiteman *et al*. 1992
	DBH 60 & WD 60	0.08	0.06	Gea *et al*. 1997
	HT 84 & DBH 84	0.90	0.79	Greaves *et al*. 1997
	HT 84 & VOL 84	0.92	0.82	
	HT 84 & WD 84	0.09	0.13	
	DBH 84 & VOL 84	0.99	0.96	

Table 2.4 continued

Eucalyptus species	Trait combination [a]	Genetic correlation (r_A) (± s.e.)	Phenotypic correlation (r_P)	Author
nitens	DBH 84 & WD 84	-0.20	0.03	Greaves *et al*. 1997
	VOL 84 & WD 84	-0.24	0.00	
	BA 72 & WD 84	-0.24 ± 0.11	---	Tibbits and Hodge, 1998
	BA 72 & PY 84	0.24 ± 0.12	---	
	WD 84 7 PY 84	0.33 ± 0.11	---	
	DBH 144 & WD 144	-0.57 ± 0.15	-0.11	Kube *et al*. 2001
	DBH 144 & CC 144	0.79 ± 0.10	0.32	
	WD 144 & CC 144	-0.45 ± 0.18	0.11	
regnans	HT 45 & VOL 45	0.83 ± 0.12	0.78	Griffin and Cotterill, 1988
	DBH 45 & VOL 45	0.98 ± 0.01	0.97	
urophylla	HT 84 & DBH 84	0.85	0.83	Mori *et al*. 1990
	HT 84 & VOL 84	0.87	0.82	
	DBH 84 & VOL 84	0.99	0.93	
	HT 60 & DBH 60	0.92 ± 0.01	0.86	Wei and Borralho, 1997
	HT 60 & VOL 60	0.92 ± 0.01	0.87	
	HT 60 & PY 72	0.04 ± 0.03	0.09	
	HT 60 & WD 72	-0.04 ± 0.04	-0.11	
	DBH 60 & VOL 60	1.0 0.00	0.98	
	DBH 60 & PY 72	0.35 ± 0.03	0.25	
	DBH 60 & WD 72	-0.36 ± 0.04	-0.23	
	VOL 60 & PY 72	0.32 ± 0.03	0.25	
	VOL 60 & WD 72	-0.34 ± 0.04	-0.22	
	PY 72 & WD 72	-1.00 ± 0.01	-0.80	
	VOL 36 & WD 36	-0.11	---	Jianzhong, 2003
	VOL 48 & WD 48	-0.06	---	
	VOL 60 & WD 60	-0.10	---	
	VOL 72 & WD 72	-0.12	---	

Table 2.4 continued

Eucalyptus species	Trait combination [a]	Genetic correlation (r_A) (± s.e.)	Phenotypic correlation (r_P)	Author
urophylla	HT 12 & DBH 12	0.75	---	Sanchez-Vargas *et al*. 2004
	HT 12 & VOL 12	0.88	---	
	DBH 12 & VOL 12	0.97	---	
	HT 36 & DBH 36	0.93	0.80	Ignacio-Sanchez *et al*. 2005
	HT 36 & VOL 36	0.93	0.85	
	HT 36 & WD 36	0.17	0.12	
	DBH 36 & VOL 36	0.98	0.97	
	DBH 36 & WD 36	-0.04	0.01	
	VOL 36 & WD 36	0.003	0.04	

* = Correlation is outside the parameter space. Sample size is too small to determine an accurate value

a = number after trait combination abbreviation is age indicated in months

b = results from three independent trials that made up the experiment

2.6 Quantitative studies of economically important traits: Genotype by environment interaction

Genotype by environment interaction (GEI) in forest tree species arises when the relative performance of genetic entries is not consistent in different environments, (Osorio *et al*. 2001). Shelbourne (1972) described GEI as being the variation among genotypes in response to different environmental conditions. Matheson (1986) concluded that GEI was the combined action of genotypes and environments. According to Matheson and Raymond (1984b), GEI is caused by a deviation in individual genotype values in a site, as a result of the additive effects of the genotypes and environments. They further state that the deviations are caused by changes in the behavior of the genotypes among different sites, or by a variation in the expression of the behavior of the genes controlling a particular trait.

As plantations cover a wide range of environmental conditions, genotypes may be expected to differ in their performance across sites. Determining the size and practical importance of GEI is critical for designing tree breeding programs and making decisions about plantation establishment (Muneri and Raymond, 2000). Knowledge of GEI is absolutely essential in determining optimum strategies for breeding and commercial forestry programs in order to determine expected genetic gains (Borralho *et al*. 1992). To select superior genotypes of multiple-site or single-site adaptability, it is important to analyze growth on different sites (Jiamin *et al*. 2003). In order to accomplish breeding value predictions, it is necessary to estimate GEI (Tibbits and Hodge, 2003).

When GEI is present, tree breeders can either develop separate breeding or commercial populations for each site type, or select genotypes that perform well across many sites (McKeand *et al*. 1990). The GEI, when it is present and its effects are ignored in tree breeding programs, may cause a reduction in genetic gains that a selection program would like to promote (Mori *et al*. 1990). In a study done on *E. urophylla*, Wei and Borralho (1998) found that by ignoring the effect of GEI reduced the expected genetic gain for growth by 27%. Where very little or no GEI exist, the tree breeder may utilize one population of good general performers and has the practical advantage of simplicity in breeding programs and then also for nursery management (Borralho *et al*. 1992). Absence of any important GEI on a regional scale will greatly simplify deployment strategies of improved seed and seedlings, and reduce costs of progeny testing (Magnussen and Yeatman, 1990).

The most popular method for analyzing GEI consists of calculating the genetic correlation (Type B) among different environments (Burdon, 1977). Although this method does not make it possible to know a detailed response of each genotype, it provides a quantitative measurement of the importance of the interaction, and consequently, of the stability of the genotypes. Furthermore, it can be used to evaluate the efficiency of selection of genotypes in a site and planting them in another, which is of practical importance (Pswarayi *et al*. 1997). Type B genetic correlation measures the degree of commonality of gene effects for a trait in two environments, and is thus a good measure of GEI (Burdon, 1977). It ranges between 0 and 1; where 1 represents perfect correspondence of genotypes across environments, i.e. zero GEI (Hodge *et al*. 1996).

Another way of explaining it is when the Type B genetic correlation decreases, an increase in GEI is expected. Shelbourne (1972) proposed a rule of thumb to judge the importance of GEI in selection programs. If the ratio of the variance due to GEI over family variance is larger than 0.5, selection efficiency would be seriously affected if GEI is ignored.

Results from various studies that examined GEI for economically important traits for some *Eucalyptus* species are presented in Table 2.5. In some studies, although GEI was investigated, the authors did not make any recommendations with regards to research and commercial deployment strategies (Brasil and Veiga, 1994; Hodge *et al*. 1996; Tibbits and Hodge, 1998; Miranda *et al*. 2001). This however does not prevent the reader, in conjunction with practical recommendations from other studies, to derive practical solutions from these results.

An observation made from the literature review is that wood properties in general, are less influenced by GEI than is the case for growth properties (Tibbits and Hodge, 1998; Muneri and Raymond, 2000; Osorio *et al*. 2001; Raymond *et al*. 2001). This is due to the fact that wood properties are generally under stronger genetic control than is the case with growth properties, where the effect of the environment is more likely to manifest itself. However, in a study done on *E. nitens*, Kube and Raymond (2002) found that the growth traits studied showed less GEI than the wood properties from the same experiment.

In certain studies (especially clonal production GEI studies), where significant or moderate GEI was observed, the authors did find out of the overall population a group of genotypes that were always superior, regardless of the environment they had been planted in (Borralho *et al*. 1992; Raymond *et al*. 2001). This is most definitely a practical solution for commercial clonal deployment strategies, but might be problematic in breeding populations. The main reason of concern here is that by making use of good generalists across a range of different environmental conditions, it is bound to reduce the genetic variation in the breeding population. This will be of concern when these genetically "narrow" populations are then used for future advanced generation breeding projects.

An interesting observation was made in a study where GEI was investigated for various traits in *E. globulus* and *E. nitens* (Hodge *et al*. 1996). The authors found that high levels of inbreeding in the breeding population are likely to mask the effect of GEI. They stipulate that inbreeding is a "hard" genetic effect, not easily altered by the environment. To explain it differently, a poor inbred individual will remain a poor inbred individual, regardless of the environment it is planted in. They advised tree breeders to view critically low or insignificant GEI levels in a tree population when the population contains a significant number of inbred individuals.

Table 2.5. Genotype by environment interactions of economically important traits measured of some *Eucalyptus* species.

Eucalyptus species	Trait	Type B genetic corr. [a]	Level of GEI declared	Author's recommendation	Author
globulus	BA	---	significant	use good generalists	Borralho *et al*. 1992
	VOL	1.00	zero	none	Hodge *et al*. 1996
	VOL	0.29	high	none	
	VOL	0.54	moderately high	none	
	VOL	0.21	high	none	
	DBH	0.80	low	use single population	MacDonald *et al*. 1997
	WD	0.91	low	use single population	
	DBH	0.39	high	use good generalists	Muneri and Raymond, 2000
	WD	0.73	low	use single population	
	WD	---	non-significant	none	Miranda *et al*. 2001
	DBH	0.39	moderately high	use good generalists	Raymond *et al*. 2001
	WD	0.73	low	use good generalists	
	PY	0.89	low	use good generalists	
	DBH	---	non-significant	use single population	Silva *et al*. 2004
	WD	---	non-significant	use single population	
grandis	VOL	0.60	moderate	use multiple populations	Osorio *et al*. 2001
	WD	0.90	low	use single population	
nitens	VOL	0.39	moderately high	none	Hodge *et al*. 1996
	VOL	0.47	moderately high	none	
	BA	0.50	moderately high	none	Tibbits and Hodge, 1998
	WD	0.97	low	none	
	PY	0.94	low	none	
	DBH	1.00	zero	use single population	Kube and Raymond, 2002
	WD	0.77	low	use single population	
	CC	0.86	low	use single population	

Table 2.5 continued

Eucalyptus species	Trait	Type B genetic corr. [a]	Level of GEI declared	Author's recommendation	Author
tereticornis	HT	---	significant	use multiple populations	Ginwal *et al*. 2004
urophylla	HT	---	significant	use multiple populations	Mori *et al*. 1990
	DBH	---	significant	use multiple populations	
	VOL	---	significant	use multiple populations	
	WD	---	non-significant	none	Brasil and Veiga, 1994
	WD	---	non-significant	use single population	Wei and Borralho, 1997
	DBH	0.66	low	use single population	
	HT	0.83	low	use single population	
	HT	---	significant	use *multiple* populations	Jiamin *et al*. 2003
	DBH	---	significant	use multiple populations	
	VOL	---	significant	use multiple populations	
	DBH	0.65	low	use single population	Sanchez-Vargas *et al*. 2004
	VOL	0.64	low	use single population	

a = Where no Type B genetic correlation estimates were presented, the authors made use of the mean squares of combined-site analysis of variance to determine if the genotype x site component of variance was significant or not

2.7 References

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CHAPTER 3. GROWTH TRAITS

3.1 Abstract

The objective of this chapter was to evaluate *Eucalyptus urophylla* S.T. Blake provenances in terms of their height, diameter and volume growth performance. Data of 9022 open-pollinated progenies representing 306 families collected from 17 provenances was used in this study. Narrow-sense heritability values were estimated for height, diameter and volume growth from this 48-month-old *E. urophylla* provenance/progeny trial planted in KwaZulu-Natal. The results show that provenances Watakika, Mainang and Apui consistently produced the highest values for the three growth traits measured. Provenances A'Esreal, Leloboko and Hokeng consistently produced the weakest performance for all three growth traits. Narrow-sense heritability was found to be moderate to weak (Height = 0.14; Diameter = 0.15; Volume = 0.17). However, this still allows for tree breeders to make significant genetic gains through accurate selection from this *E. urophylla* breeding population.

Key words: *Eucalyptus urophylla*, provenance, height, diameter, volume, narrow-sense heritability

3.2 Introduction

Eucalyptus urophylla has a natural distribution that is restricted to seven islands of the lesser Sunda Archipelago in Indonesia: Flores, Adonara, Lembata, Pantar, Alor, Wetar and Timor. Its latitudinal range is 7°30'-10°00' south, with a longitudinal range of 122°00'-127°00 east. It occurs predominantly between 300 and 1100m above sea level, although smaller groups of trees grow at altitudes as high as 3000m above sea level. *Eucalyptus urophylla* may be successfully grown as a pure species, or as a hybrid with *Eucalyptus grandis* Hill ex Maiden, at low altitudes where few other *Eucalyptus* species grow successfully (Gunn *et al.*, 1995). In the last decade or two, *E. urophylla* has become increasingly important for wood production in plantations at low altitude sites in seasonally dry tropics to subtropics. Its widespread adoption arose from outstanding performances in the Congo and Brazil where it proved to be much more resistant to disease than *E. grandis*, while still having good growth characteristics.

In South Africa, *E. urophylla* is predominantly used as a hybrid parent with *E. grandis*, to produce the commercially successful hybrid E. gra X E. uro (GU). This hybrid combination plays a very important role in producing raw material for the Kraft pulping process in the country. Although *E. urophylla* is extensively used as a hybrid partner in the South African forestry industry, very little published information is available regarding the genetics and use of this species in South Africa. Other than work done by Darrow and Roeder (1983), no other genetic analyses from South Africa have been published.

The aim of this chapter was to add information to this limited knowledge base by investigating the level of genetic control for growth traits in a large *E. urophylla* breeding population grown in South Africa.

3.3 Materials and methods

3.3.1 Genetic material

During 1998 the CAMCORE Co-operative, in conjunction with P.T. Surya Hutani Jaya, made joint seed collections of *Eucalyptus urophylla* in Indonesia. Seed from 306 mother trees representing 17 provenances were collected. Information of the provenances used in this study is provided in Table 3.1. This collection represents one of the most complete and widespread that has ever been made on *E. urophylla*. During 1999, the seed was sown at the Mondi Mountain Home nursery (Hilton), and later in the year, a field trial of open-pollinated *E. urophylla* provenance/progeny seed lots were established in northern KwaZulu-Natal, South Africa.

Table 3.1. Provenance information represented by families in the study

Provenance name	Latitude (S)	Longitude (E)	Altitude range (m)	Number of families
A' Esreal	9° 36'	124° 14'	1750-1800	9
Apui	8° 16'	124° 44'	1100-1300	20
Fatumnase	9° 34'	124° 13'	1700-2000	4
Hokeng	8° 31'	122° 47'	350-800	27
Ille Nggele	8° 39'	122° 26'	610-800	23
Kilawair	8° 41'	122° 29'	225-530	20
Lere Baukrenget	8° 39'	122° 23'	700-750	18
Lelobatang I	9° 41'	124° 14'	1200-1400	11
Lelobatang II	9° 43'	124° 10'	1400-1650	26
Leloboko	9° 37'	124° 10'	1400-1600	11
Mainang	8° 14'	124° 39'	1100-1250	20
Mollo	9° 41'	124° 11'	1200-1600	19
Naususu	9° 38'	124° 13'	1200-1450	20
Pintu Mas	8° 17'	124° 33'	320-450	20
Tune	9° 33'	124° 19'	1100-1400	20
Tutem	9° 35'	124° 17'	1200-1400	18
Watakika	8° 18'	124° 30'	350-600	20

3.3.2 Test site information

The site selected for the field trial represents a typical target environment for GU hybrid clonal plantations in South Africa. Such an environment will typically be humid tropical to sub-tropical, in summer rainfall areas, with very little or zero frost, extended dry periods during winter and deep, well-drained soils. Table 3.2 provides location and climatic information of the site utilized in this study.

Table 3.2. Location and climatic conditions of *Eucalyptus urophylla* provenance/progeny field trial

Map Key[1]	Geographic location	Mondi farm	Latitude (S)	Longitude (E)	Altitude (m)	MAP (mm)	MAT (°C)
1	Northern KwaZulu Natal	Flatcrown	28° 33’	32° 07’	71	1008	21.6

1 = key to field trial location in Figure 3.1; MAP = mean annual precipitation; MAT = mean annual temperature.

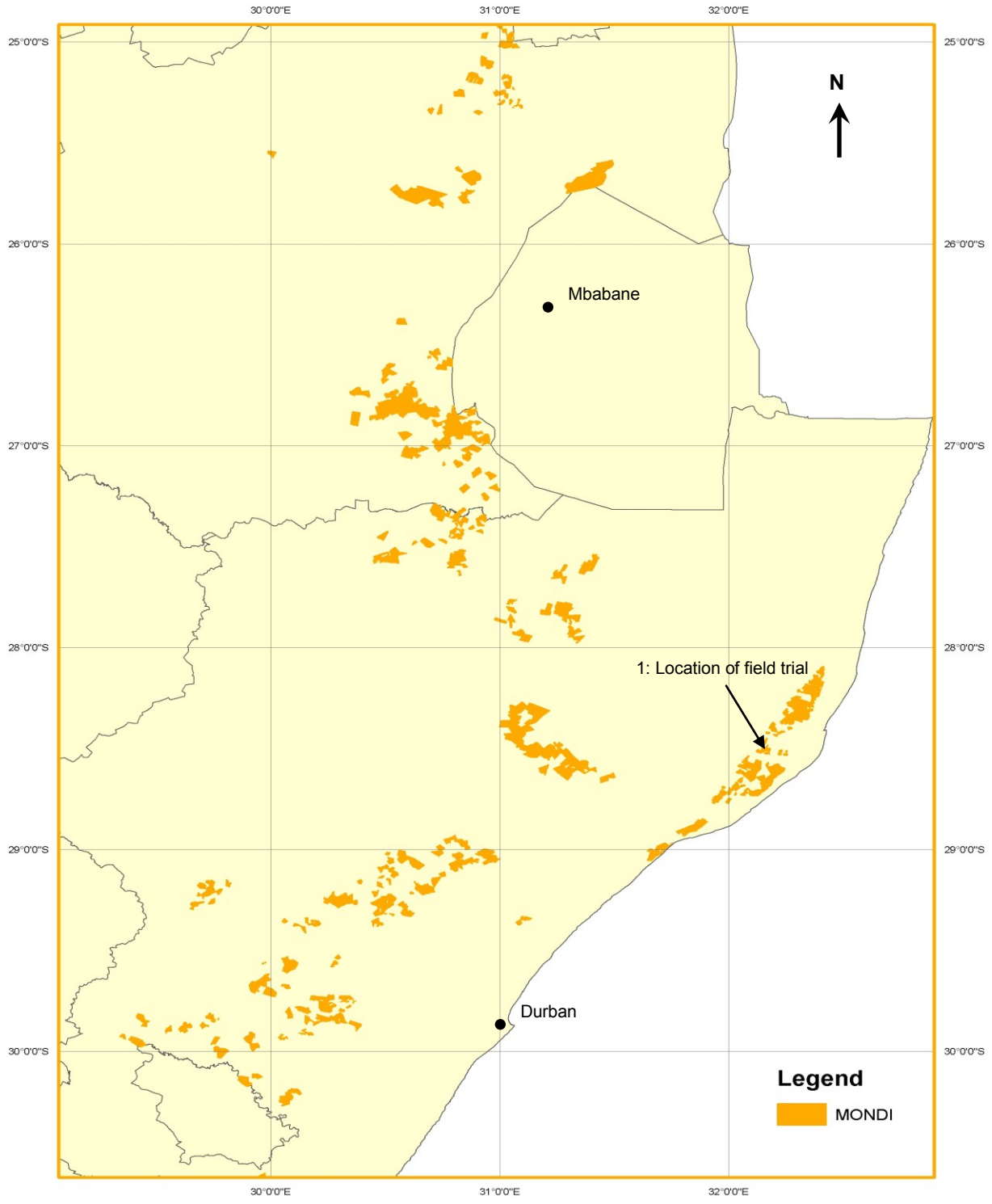

Figure 3.1 Location of field trial

3.3.3 Field trial design

The trial design was a randomized complete block with five replicates and 1 x 6 tree row plots. Within each replicate, families from the same provenance were randomly blocked together, with each provenance block randomly distributed across the five replicates.

Trees were established at a 3m x 2m espacement, giving a total of 1667 trees per hectare. Silviculture treatments such as pre-plant site preparation, planting, fertilizer application and weeding were all done to similar commercial standards as required by Mondi plc. The design, in-field layout and silviculture treatments were all applied in such a manner to reduce the environmental variation between trees to a minimum.

3.3.4 Data collection of growth traits

The first sets of data collected for this study were tree height and diameter. Data was collected from all trees at an age of 48 mo. Total tree height (HT) was measured with a Vertex hypsometer. Diameter at breast height (DBH) was measured with a diameter tape. Individual tree volumes were estimated by using the following volume equation developed for *Eucalyptus* seedlings by the Forest Technical Department of Mondi.

Individual Tree Volume (m^3) = (3.1415927/40000).k.DBH^2.HT ……[**1**]

Where k = (B/3)+(A/2)-(A+B)+((C/3).E)+((D/3).F)

And A = -2.55302 D = 228.6886

B = 1.115693 E = 0.583127

C = -0.75464 F = 0.000068

3.3.5 Data editing

Prior to analysis, editing of the data was performed to remove measurements of recording errors as well as measurements from runts. The identification of potential outliers and influential measurements was conducted by making use of linear regression models for diameter and height, diameter and volume as well as height and volume, using PROC REG (SAS ®). This procedure allowed the plotting of all observations and provided useful information on measurements for outliers as well as their effects on the moments of the distribution, i.e., mean, error variance, skewness and kurtosis.

Due to the fact that provenance effects were estimated, controls planted in the field trial were excluded from the analysis of variance. The first reason for this is that each control did not represent a pure provenance *per se*, but was made up of imported material selected from parents representing a wide range of different provenances. Secondly, as the number of trees representing each control was much smaller when compared to the number of trees representing each provenance, controls were excluded from the analysis of data. Individual trees with a height equal or less than 4 m or with a diameter

equal or less than 40 mm were deemed as runts and hence excluded from the analysis (this represents a total of 4.5% of all measured trees).

3.3.6 Data analysis

Provenance effects and genetic parameters for volume, height and diameter growth were estimated by making use of data from 9022 trees measured in the field trial.

Analysis of variance (ANOVA) was conducted and F-statistics were calculated to determine whether significant differences among provenances exist. Secondly, from this ANOVA, components of variance were calculated for later estimation of genetic parameters. Analysis was conducted using the General Linear Model procedure of SAS®, where variance components were estimated using TYPE III output. The following linear model was used for growth data analysis.

$$Y_{jklm} = \mu + r_j + p_k + r(p)_{jk} + f(p)_{kl} + r*f(p)_{jkl} + \varepsilon_{jklm} \quad \text{.....[2]}$$

Where:

- Y_{jklm} = phenotypic observation from the jklmth tree
- μ = overall mean in the test
- r_j = random effect of the jth replicate within the test; $E(r_j) = 0$ and $Var(r_j) = \sigma^2_r$
- p_k = random effect of the kth provenance; $E(p_k) = 0$ and $Var(p_k) = \sigma^2_p$
- $r(p)_{jk}$ = random effect due to interaction of the jth replicate with the kth provenance; $E(r(p)_{jk}) = 0$ and $Var(r(p)_{jk}) = \sigma^2_{rp}$
- $f(p)_{kl}$ = random effect of the lth family in the kth provenance; $E(f(p)_{kl}) = 0$ and $Var(f(p)_{kl}) = \sigma^2_f$
- $r*f(p)_{jkl}$ = random effect due to interaction of the jth replicate with the lth family within the kth provenance; $E(r*f(p)_{jkl}) = 0$ and $Var(r*f(p)_{jkl} = \sigma^2_{r*f(p)}$
- ε_{jklm} = random error term associated with the jklmth tree; $E(\varepsilon_{jklm}) = 0$ and $Var(\varepsilon_{jklm}) = \sigma^2_\varepsilon$

Table 3.3 provides a skeleton format of the ANOVA table derived from making use of the above linear model to analyze the growth data.

Table 3.3. Skeleton format of ANOVA table

Source of Variation	**d.f.**	**MS**	**EMS**
Replication	r-1	MS_1	$\sigma^2_\varepsilon + n\sigma^2_{r*f(p)} + nf\sigma^2_{rp} + npf\sigma^2_r$
Provenance	p-1	MS_2	$\sigma^2_\varepsilon + n\sigma^2_{r*f(p)} + nr\sigma^2_f + nf\sigma^2_{rp} + nrf\sigma^2_p$
Rep * Provenance	(r-1) (p-1)	MS_3	$\sigma^2_\varepsilon + n\sigma^2_{r*f(p)} + nf\sigma^2_{rp}$
Family (Provenance)	p (f-1)	MS_4	$\sigma^2_\varepsilon + n\sigma^2_{r*f(p)} + nr\sigma^2_f$
Rep * Fam (Prov)	pr (f-1)	MS_5	$\sigma^2_\varepsilon + n\sigma^2_{r*f(p)}$
Within plot	prf (n-1)	MS_6	σ^2_ε

Where:

- r = number of replicates
- p = number of provenances
- f = number of families per provenance
- n = number of trees per plot
- σ^2_ε = within plot variance (sampling error)
- $\sigma^2_{r*f(p)}$ = plot variance
- σ^2_f = family within provenance variance
- σ^2_{rp} = replication x provenance variance
- σ^2_p = provenance variance
- σ^2_r = replication variance

3.3.7 F-test calculations

F-Statistics were calculated to examine if the provenance term was significant for volume, height and diameter growth. For each F-test calculated, the null hypothesis (H_o) stated there were no significant differences between the provenance means for each growth trait measured. The alternative hypothesis (H_a) stated that at least one of the provenance means differed significantly from the rest. To test if the provenance term was significant, Satterthwaite's quasi-F ratio was used, as suggested by Steel and Torrie (1980, p. 357), and is shown below.

F ratio for the provenance term is:

$$F_{p,q} = \frac{MS_2 + MS_5}{MS_3 + MS_4} \quad \text{.....[3]}$$

where p & q are the effective degrees of freedom to be used in testing the calculated F ratio. The formulas used to calculate these two effective degrees of freedom are shown below.

$$p = \frac{(MS_2 + MS_5)^2}{\frac{(MS_2)^2}{(p-1)} + \frac{(MS_5)^2}{pr(f-1)}} \quad \text{.....[4]}$$

and

$$q = \frac{(MS_3 + MS_4)^2}{\frac{(MS_3)^2}{(r-1)(p-1)} + \frac{(MS_4)^2}{p(f-1)}} \quad \text{.....[5]}$$

3.3.8 Variance component calculations

The calculation of variance components is an important step to determine accurate genetic parameters such as heritability, genetic and phenotypic correlations as well as predicted genetic gains. The objective here is to partition the variation found in the analysis into components attributable to different causes.

As mentioned earlier, ANOVA was conducted using the General Linear Model procedure of SAS®, where variance components were estimated using TYPE III output. Variance components due to replications (σ^2_r), provenances (σ^2_p), replication x provenance interaction (σ^2_{rp}), families (σ^2_f), replication x family within provenance interaction ($\sigma^2_{r*f(p)}$) and within-plot error (σ^2_ε) were calculated from the expectations of mean squares as indicated in Table 3.4.

Table 3.4. Components of variance calculation

Variance component	Symbol	Method of calculation
Replications	σ^2_r	$(MS_1 – MS_3) / npf$
Provenances	σ^2_p	$(MS_2 – MS_3 – MS_4 + MS_5) / nrf$
Rep x Prov interaction	σ^2_{rp}	$(MS_3 – MS_5) / nf$
Families	σ^2_f	$(MS_4 – MS_5) / nr$
Rep x Fam(Prov) interaction	$\sigma^2_{r*f(p)}$	$(MS_5 – MS_6) / n$
Within-Plot error	σ^2_ε	MS_6

where:

- r = number of replicates
- p = number of provenances
- f = number of families per provenance
- n = number of trees per plot

It is important to note, as mentioned earlier, that when variance components are estimated on a single-site basis, family-by-environment interaction variance cannot be estimated, and in fact they are added to the estimate of family variance (σ^2_f) on that particular site. Thus, the estimate of variance among families includes both σ^2_f and σ^2_{fe}, and has been referred to as “biased” since it does not only estimate σ^2_f (Comstock and Moll, 1963). The implication of this biased effect is that later calculations of single-site heritabilities will be inflated due to the presence of family-by-environment interaction variance within family variance (White and Hodge, 1990).

3.3.9 Narrow-sense heritability estimates

From the breakdown of the total variation into its different components (as done in the previous section), it is possible to calculate the phenotypic variance within-provenance (σ^2_T) as follows:

$$\sigma^2_T = \sigma^2_f + \sigma^2_{r*f(p)} + \sigma^2_\varepsilon \quad \text{.....[6]}$$

where:

- σ^2_f = variance due to the random effect of the l^{th} family in the k^{th} provenance
- $\sigma^2_{r*f(p)}$ = variance due to the random interaction effect of the j^{th} replication with the l^{th} family within the k^{th} provenance
- σ^2_ε = variance due to the random error term associated with the $jklm^{th}$ tree

From this, single-site (biased) narrow-sense heritability estimates within provenance (h^2) were estimated for all growth traits assessed, using the following formula:

$$h^2 = (2.5*\sigma^2_f) / \sigma^2_T \quad \text{.....[7]}$$

A coefficient of 2.5 instead of 4 was multiplied with the family variance to give an estimate of the additive genetic variance. The choice of the coefficient of 2.5 in the calculation of narrow-sense heritability is commonly used by many authors working with *Eucalyptus* (Volker *et al*., 1994), and assumes an average rate of out-crossing of 70% for *Eucalyptus* species (Morgan and Bell, 1983; Griffin and Cotterill, 1988).

Standard errors for the narrow-sense heritability estimates were calculated according to Becker (1985), as:

$$\sigma_{(h^2)} = 2.5 * \sqrt{[2 * (1 - t)^2 * (1 + (k - 1) * t)^2] / [k * (k - 1) * (s - 1)]} \quad \text{.....[8]}$$

Where:

- k = number of offspring per family
- s = number of families
- $t = h^2 / 2.5$

3.4 Results

Results from single-site analysis of variance for growth traits height, diameter and volume are presented in Tables 3.5, 3.6 and 3.7, respectively. Together with this is a summary of the hypothesis tests which investigated the provenance effect for height, diameter and volume growth, presented in Table 3.8.

Table 3.5. Single-site analysis of variance for height growth (HT)

Source of variation	**df**	**SS**	**MS**	**F**	**Prob.** [a]
Replicate	4	8.8968	2.2242	0.09	0.9842 ns
Provenance	16	3788.6039	236.7877	9.97	<.0001 **
Rep * Provenance	64	1520.7116	23.7611	2.55	<.0001 **
Family (Provenance)	289	6250.7384	21.6289	2.32	<.0001 **
Rep * Fam(Provenance)	1155	10767.4537	9.3225	1.26	<.0001 **
Error	6844	50502.7558	7.3791		
Total	8372	72874.8758			

a: ns = not significant if prob. > 0.05; * = significant if prob. < 0.05; ** = highly significant if prob. < 0.01

Table 3.6. Single-site analysis of variance for diameter growth (DBH)

Source of variation	df	SS	MS	F	Prob. [a]
Replicate	4	285.2874	71.3218	3.09	0.0218 *
Provenance	16	3499.6087	218.7255	9.47	<.0001 **
Rep * Provenance	64	1477.9045	23.0923	1.97	<.0001 **
Family (Provenance)	289	8107.6967	28.0543	2.40	<.0001 **
Rep * Fam(Provenance)	1155	13526.1372	11.7109	1.23	<.0001 **
Error	6844	65036.0404	9.5026		
Total	8372	92080.5170			

a: ns = not significant if prob. > 0.05; * = significant if prob. < 0.05; ** = highly significant if prob. < 0.01

Table 3.7. Single-site analysis of variance for volume growth

Source of variation	df	SS	MS	F	Prob. [a]
Replicate	4	0.0206	0.0052	1.56	0.1960 ns
Provenance	16	0.6266	0.0392	11.85	<.0001 **
Rep * Provenance	64	0.2114	0.0033	2.41	<.0001 **
Family (Provenance)	289	1.0456	0.0036	2.64	<.0001 **
Rep * Fam(Provenance)	1155	1.5832	0.0014	1.20	<.0001 **
Error	6844	7.8000	0.0011		
Total	8372	11.3279			

a: ns = not significant if prob. > 0.05; * = significant if prob. < 0.05; ** = highly significant if prob. < 0.01

Table 3.8. Summary of hypothesis tests that investigated provenance effect for growth traits

Trait	**$F_{calc.}$**	**$F_{tab.}$**	**$F_{calc.} > F_{tab}$?**	**Accept / reject H_o?**
Height	5.42	1.71	Yes	Reject H_0 and accept H_a
Diameter	4.51	1.61	Yes	Reject H_0 and accept H_a
Volume	5.86	1.71	Yes	Reject H_0 and accept H_a

H_o: $\mu_1 = \mu_2 = \mu_3 = \ldots = \mu_i$

H_a: At least one of the provenances differs significantly from the rest

$p = 0.05$

From the above analysis of variance of growth traits, together with the hypothesis tests for the effect of provenances, it appears that for this *E. urophylla* breeding population, there are significant differences between the provenances for the growth traits height, diameter and volume, measured at an age of 48 mo. Tables 3.9, 3.10 and 3.11 indicate the average provenance performance of height, diameter and volume growth, respectively.

Table 3.9. Mean provenance results for 48 mo height (m) growth

Provenance	Height (± s.e.) (m)	Number of observations	Waller grouping [a]
Mainang	13.229 (± 2.67)	520	A
Watakika	13.219 (± 3.60)	558	A
Apui	13.201 (± 2.69)	537	A
Fatumnase	13.093 (± 2.12)	112	A B
Tutem	13.064 (± 2.68)	513	A B
Ille Nggele	13.064 (± 2.57)	623	A B
Pintu Mas	13.005 (± 3.20)	548	A B
Tune	12.908 (± 2.76)	564	A B
Kilawair	12.894 (± 2.56)	577	A B
Lere Baukrenget	12.850 (± 2.93)	503	B
Lelobatang I	12.456 (± 3.19)	280	C
Naususu	12.443 (± 3.19)	537	C
Mollo	11.820 (± 2.98)	541	D
Lelobatang II	11.705 (± 2.36)	719	D E
Hokeng	11.683 (± 3.27)	725	D E
Leloboko	11.369 (± 2.69)	302	E
A' Esreal	10.970 (± 2.59)	234	F

a = Provenances without common letters are significantly different at the 95% significant level

Table 3.10. Mean provenance results for 48 mo diameter (mm) growth

Provenance	Diameter (± s.e.) (mm)	Number of observations	Waller grouping [a]
Watakika	120.022 (± 30.19)	558	A
Apui	110.709 (± 30.09)	537	A B
Pintu Mas	110.683 (± 30.66)	550	A B
Mainang	110.646 (± 40.01)	520	A B C
Fatumnase	110.472 (± 20.63)	112	B C
Kilawair	110.419 (± 20.97)	560	B C
Ille Nggele	110.399 (± 30.08)	624	B C
Tutem	110.369 (± 30.01)	513	B C
Lere Baukrenget	110.289 (± 30.34)	506	C
Tune	110.263 (± 30.12)	564	C
Naususu	100.857 (± 30.40)	537	D
Lelobatang I	100.771 (± 30.39)	280	D E
Mollo	100.392 (± 30.26)	541	E F
Lelobatang II	100.305 (± 20.67)	720	F
Leloboko	100.263 (± 20.98)	302	F
Hokeng	100.114 (± 30.74)	726	F
A' Esreal	90.680 (± 20.80)	234	G

a = Provenances without common letters are significantly different at the 95% significant level

Table 3.11. Mean provenance results for 48 mo volume (m³) growth

Provenance	Volume (± s.e.) (m^3)	Number of observations	Waller grouping [a]
Mainang	0.0698 (± 0.046)	520	A
Watakika	0.0682 (± 0.040)	558	A B
Pintu Mas	0.0671 (± 0.046)	548	A B
Apui	0.0642 (± 0.035)	537	B C
Lere Baukrenget	0.0604 (± 0.039)	503	C D
Ille Nggele	0.0603 (± 0.033)	623	C D
Tutem	0.0601 (± 0.035)	513	C D
Fatumnase	0.0592 (± 0.033)	112	D E
Tune	0.0592 (± 0.037)	564	D E
Kilawair	0.0591 (± 0.032)	557	D E
Naususu	0.0555 (± 0.038)	537	E F
Lelobatang I	0.0546 (± 0.036)	280	F
Hokeng	0.0482 (± 0.038)	725	G
Mollo	0.0481 (± 0.031)	541	G
Lelobatang II	0.0440 (± 0.024)	719	G H
Leloboko	0.0439 (± 0.027)	302	H
A' Esreal	0.0379 (± 0.024)	234	I

a = Provenances without common letters are significantly different at the 95% significant level

The partitioning of the total phenotypic variances for the growth traits height, diameter and volume into their various components are presented in Table 3.12. Variance components are calculated from the expected mean squares derived from the analysis of variance.

Table 3.12. Components of variation for height, diameter and volume growth

Trait	**Components of variation** [a]					
	Provenances	**Families**	**Rep x Provenance**	**Rep x Fam(Prov.)**	**Replications**	**Within – plot error**
Height	0.5233 (5.9)	0.4639 (5.2)	0.1882 (2.1)	0.3663 (4.1)	0.0000 (0.0)	7.3791 (82.7)
Diameter	0.4679 (4.2)	0.6163 (5.5)	0.1484 (1.3)	0.4162 (3.7)	0.0023 (0.02)	9.4963 (85.2)
Volume	0.000088 (6.6)	0.000085 (6.3)	0.000025 (1.9)	0.000044 (3.3)	0.000001 (0.0)	0.0011 (81.9)

a = Percentage in parenthesis

The within-provenance phenotypic variance for all three growth traits was calculated from the breakdown of the total variation into its different components, as shown in Table 3.12. From this, single-site (biased) narrow-sense heritabilities were estimated for all three growth traits. The within-provenance phenotypic variance as well as the within-provenance heritabilities for height, diameter and volume growth is presented in Table 3.13. Standard errors for the narrow-sense heritability estimates are also included.

Table 3.13. Within-provenance phenotypic variance as well as within-provenance heritabilities (±s.e.) for height, diameter and volume growth assessed at an age of 48 mo

Trait	Within – provenance phenotypic variance	Within – provenance heritability (± s.e.)
Height	8.2086	0.14 (± 0.018)
Diameter	10.5341	0.15 (± 0.019)
Volume	0.0013	0.17 (± 0.020)

3.5 Discussion

From the analysis of variance, it is clear that for this *E. urophylla* breeding population, there are significant differences between the provenances for the growth traits height, diameter and volume. These results identify those provenances that produced the highest growth. The results show that in this breeding population, the provenances Watakika, Mainang and Apui consistently produced the highest values for the three important growth traits, whereas A'Esreal, Leloboko and Hokeng consistently produced the weakest performance for the three growth traits.

For all three growth traits, within-plot variation was the major source of variation (82-85% of the total phenotypic variance). This variation pattern is not uncommon in genetic tests of forest tree species. Another observation made is that the effect of replicates is virtually zero and is indicative of a homogeneous test site. Although replicate-by-provenance and replicate-by-family within provenance interactions were statistically

significant for all three growth traits, their variance components are small when compared to variance due to provenances and families.

Narrow-sense heritabilities for all three growth traits were found to be moderate to weak. However, this gives tree breeders the opportunity to make significant genetic gains through accurate selection from this *E. urophylla* breeding population. These narrow-sense heritabilities compare favorable to narrow-sense heritability estimates from another *E. urophylla* experiment conducted by Wei and Borralho (1998). For similar growth traits at relatively similar ages of measurement, they estimated narrow-sense heritabilities which were slightly higher than those found here. However, if one takes into consideration that the coefficient of relationship assumed for open pollinated progeny used by Wei and Borralho (1998), was 3.3, compared to 2.5 used here, then the estimated narrow-sense heritabilities would be very similar.

3.6 References

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CHAPTER 4. WOOD AND FIBER TRAITS

4.1 Abstract

The objective of this chapter was to evaluate *Eucalyptus urophylla* S.T. Blake provenances in terms of their basic wood density and pulp yield properties. Data of 300 open-pollinated progenies representing 30 selected families from 11 provenances was used in this study. Narrow-sense heritability was estimated for basic wood density and pulp yield from a 54-month old *E. urophylla* provenance/progeny trial planted in KwaZulu-Natal. The results showed that significant provenance effects for both basic wood density and pulp yield were observed. Provenances Lere-Baukrenget, Mainang and Hokeng consistently produced the highest values for basic wood density, whilst provenances Lelobatan and Kilawer delivered the highest values for pulp yield. Narrow-sense heritability was found to be strong for basic wood density (h^2 = 0.51) and moderate to weak for pulp yield (h^2 = 0.11). This suggests that big genetic gains can be achieved for basic wood density. Although the narrow-sense heritability for pulp yield was weaker, this still allows for tree breeders to make significant genetic gains through accurate selection from this *E. urophylla* breeding population.

Key words: *Eucalyptus urophylla*, provenance, selected families, basic wood density, pulp yield, narrow-sense heritability

4.2 Introduction

The properties of wood affect the overall profitability of a pulping enterprise and end-product value (Raymond and Schimleck, 2002).

Relationships between wood properties and profitability of Kraft pulp production are well established, and studies have identified basic wood density and pulp yield as key variables (Dean *et al*. 1990; Borralho *et al*. 1993; Greaves *et al*. 1997). Not only volume growth but also basic wood density and pulp yield have a great influence in cellulose productivity. It is therefore important to include basic wood density and pulp yield as selection criteria in a tree breeding program that is aligned towards optimum cellulose production for the pulp and paper industry (Bison *et al*. 2005).

Eucalyptus is one of the best hardwoods for producing a wide range of high quality bleached papers. Delignification and separation of wood fibers as well as bleaching can be achieved with high levels of cellulose yield, coupled with low levels of chemical and energy consumption. Thus, the challenge to tree improvement programs is to select trees that will produce a high cellulose output as well as improving processing profitability (Valente *et al*. 1992).

Eucalyptus urophylla is extensively used as a hybrid partner in the South African forestry industry and plays an important role in providing raw-material for the Kraft pulping process. However, the genetics of basic wood density and pulp yield of *E. urophylla* grown in South Africa has not been studied in great detail. The first aim of this chapter

was to determine whether there are differences between *E. urophylla* provenances for basic wood density and pulp yield that will allow for selection to improve these two traits. The second aim of this chapter was to investigate the level of genetic control that exists for basic wood density and pulp yield in a large *E. urophylla* breeding population grown in South Africa.

4.3 Materials and methods

4.3.1 Genetic material

Data of wood samples collected from 300 open-pollinated progenies representing 30 selected families and 11 provenances were used in this study. Information on the provenances used in this study is provided in Table 4.1. The selected families and provenances formed part of a greater *E. urophylla* breeding population that contained 9022 open-pollinated progenies representing 306 families from 17 provenances. The families and provenances used in this study were selected on the basis of their superior growth performance shown in the greater breeding population. Screened Individuals from these families and provenances were however randomly selected for growth.

Table 4.1. Provenance information represented by families in the study

Provenance name	Latitude (S)	Longitude (E)	Altitude range (m)	Number of families
Hokeng	8° 31’	122° 47’	350-800	2
Ille Nggele	8° 39’	122° 26’	610-800	6
Kilawair	8° 41’	122° 29’	225-530	3
La Cascada Colombia	---	---	---	1
Lere-Baukrenget	8° 39’	122° 23’	700-750	7
LelobatanI	9° 41’	124° 14’	1200-1400	2
Mainang	8° 14’	124° 39’	1100-1250	3
Mondi bulk	---	---	---	1
Naususu	9° 38’	124° 13’	1200-1450	2
Tune	9° 33’	124° 19’	1100-1400	2
Tutem	9° 35’	124° 17’	1200-1400	1

4.3.2 Test site information

The site selected for the field trial represents a typical target environment for *E. grandis x E. urophylla* (GU) hybrid clonal plantations in South Africa. Such an environment is typically humid, tropical to sub-tropical, summer rainfall areas, with very little or zero frost, extended dry periods during winter and deep, well-drained soils. Table 4.2 provides location and climatic information on the site utilized in this study.

Table 4.2. Location and climatic conditions of *Eucalyptus urophylla* provenance/progeny field trial

Map Key[1]	Geographic location	Mondi farm	Latitude (S)	Longitude (E)	Altitude (m)	MAP (mm)	MAT (°C)
1	Northern KwaZulu-Natal	Flatcrown	28° 33’	32° 07’	71	1008	21.6

1 = key to field trial location in Figure 4.1; MAP = mean annual precipitation; MAT = mean annual temperature.

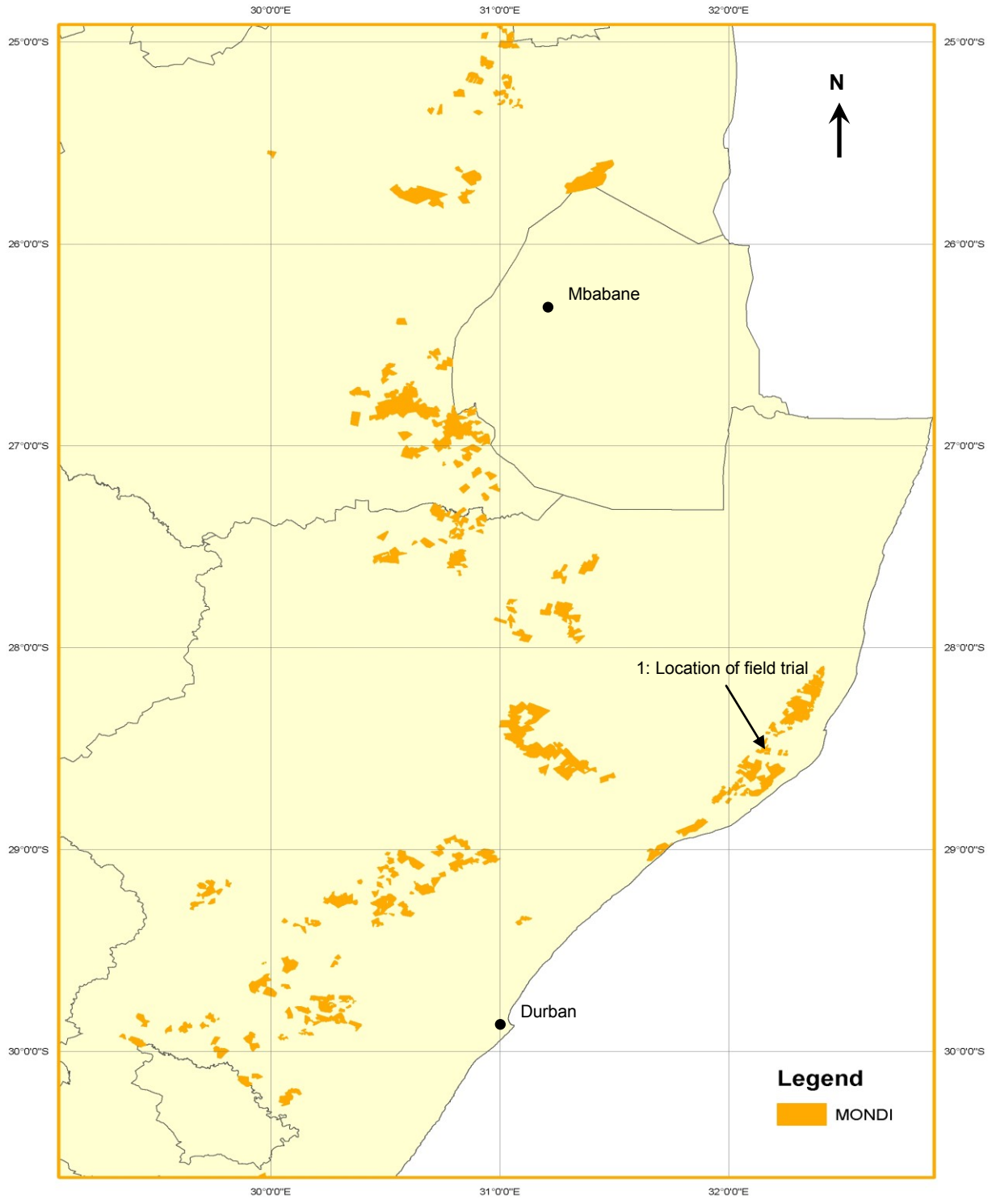

Figure 4.1 Location of field trial

4.3.3 Wood sampling and data collection

The collection of wood samples was done when the trees were 54 mo old. Each of the 30 families used in this study had 10 trees randomly sampled in order to screen the provenances for basic wood density and pulp yield performance.

Collection of wood samples for this study was done on a destructive basis by felling the selected trees, after which wood disks were removed. Whole disks were removed from each tree, starting at the base of the tree and thereafter at every 1m interval up the length of the tree, until a top diameter of 50mm was reached. At every 1m interval, including the base-cut, two 20mm thick disks were removed. The first disk of each cut-interval was used to screen basic wood density, while the second disk was used to screen pulp yield. All the disks sampled per tree for basic wood density was bagged together so that a cone-shaped sample was available for screening. The same bagging process was followed to collect material for screening of pulp yield. An example of such cone-shaped samples is provided in Figure 4.2.

Figure 4.2. Cone-shaped samples collected from an individual tree to screen for basic wood density and pulp yield.

Basic wood density is defined as oven-dry wood mass per unit volume of green wood (Kube and Raymond, 2002). Volumes of the green (water-saturated) samples were measured using the water displacement method, and the oven-dry weight of each sample was then determined after drying at 105°C for 10 hours. The volumes and oven-dry weights were used in the following model to determine basic wood density.

$$D = (W / V) * 1000 \quad \text{.....[9]}$$

Where:

- D = basic wood density ($kg.m^{-3}$)
- W = oven-dry weight of the sample (g)
- V = volume of the water-saturated sample (ml^3)

Pulp yield is defined as the proportion of dry mass recovered as pulp to the total dry mass of wood used in the pulping process (Beadle *et al*. 1996). Kraft pulping involves cooking wood chips in an alkaline solution at an elevated temperature and pressure to dissolve lignin, leaving intact fibers that are composed of cellulose and hemicelluloses (Smook, 1982).

For this study, the disks selected for the screening of pulp yield were chipped using a laboratory guillotine chipper. All wood chips derived from the disks of the same tree were mixed. This allowed selection of a composite sample of wood chips that were a true representation of the whole tree. Each tree was individually pulped in a rotating Aurora laboratory digester. Figure 4.3 presents a photograph of such a digester used in this study.

The resultant pulp from this cooking process was screened using a Packer screen with 0.8mm slots. Pulp yield was calculated as a percentage of the oven-dry mass of wood used to charge the digester.

Figure 4.3. Rotating Aurora laboratory digester used in this study to pulp wood chips.

The wood chip samples were pulped under the following conditions:

- 1000g of oven-dry wood
- 15% active alkali as NaOH based on the oven-dry wood
- Kraft cooking liquor with a Sulphidity of 25%
- Liquor to wood ratio of 4.6 : 1
- Pulping temperature of 170°C
- Ambient to 170°C in 90 minutes
- Degassing at 90°C and 105°C
- H-factor of 900

4.3.4 Data editing

Prior to analysis, editing of the data was performed. The identification of potential outliers and influential measurements was conducted by making use of linear regression models for basic wood density and pulp yield, using PROC REG (SAS ®). This procedure allowed the plotting of all observations and provided useful information on measurements for outliers as well as their effects on the moments of the distribution, i.e., mean, error variance, skewness and kurtosis. As a result of this editing, a total of one basic wood density observation and five pulp yield observations were excluded from the dataset. This represents 1% of all data points observed.

4.3.5 Data analysis

Provenance effects and genetic parameters for basic wood density and pulp yield were estimated by making use of data from 300 trees sampled in the study.

Analysis of variance (ANOVA) was conducted and F-statistics were calculated to determine whether significant differences among provenances exist. Secondly, from this ANOVA, components of variance were calculated for later estimation of genetic parameters. Analysis was conducted using the General Linear Model procedure of SAS®, where variance components were estimated using TYPE III output. The following linear model was used for basic wood density and pulp yield analysis.

$$Y_{jklm} = \mu + r_j + p_k + r(p)_{jk} + f(p)_{kl} + r*f(p)_{jkl} + \varepsilon_{jklm} \text{ ……..……[} \mathbf{10} \text{]}$$

Where:

- Y_{jklm} = phenotypic observation from the jklmth tree
- μ = overall mean in the test
- r_j = random effect of the jth replicate within the test; $E(r_j) = 0$ and $Var(r_j) = \sigma^2_r$
- p_k = random effect of the kth provenance; $E(p_k) = 0$ and $Var(p_k) = \sigma^2_p$
- $r(p)_{jk}$ = random effect due to interaction of the jth replicate with the kth provenance; $E(r(p)_{jk}) = 0$ and $Var(r(p)_{jk}) = \sigma^2_{rp}$
- $f(p)_{kl}$ = random effect of the lth family in the kth provenance; $E(f(p)_{kl}) = 0$ and $Var(f(p)_{kl}) = \sigma^2_f$
- $r*f(p)_{jkl}$ = random effect due to interaction of the jth replicate with the lth family within the kth provenance; $E(r*f(p)_{jkl}) = 0$ and $Var(r*f(p)_{jkl} = \sigma^2_{r*f(p)}$
- ε_{jklm} = random error term associated with the jklmth tree; $E(\varepsilon_{jklm}) = 0$ and $Var(\varepsilon_{jklm}) = \sigma^2_\varepsilon$

Table 4.3 provides a skeleton format of the ANOVA table derived from making use of the above linear model to analyze the growth data.

Table 4.3. Skeleton format of ANOVA table

Source of Variation	**d.f.**	**MS**	**EMS**
Replication	r-1	MS_1	$\sigma^2_\varepsilon + n\sigma^2_{r*f(p)} + nf\sigma^2_{rp} + npf\sigma^2_r$
Provenance	p-1	MS_2	$\sigma^2_\varepsilon + n\sigma^2_{r*f(p)} + nr\sigma^2_f + nf\sigma^2_{rp} + nrf\sigma^2_p$
Rep * Provenance	(r-1) (p-1)	MS_3	$\sigma^2_\varepsilon + n\sigma^2_{r*f(p)} + nf\sigma^2_{rp}$
Family (Provenance)	p (f-1)	MS_4	$\sigma^2_\varepsilon + n\sigma^2_{r*f(p)} + nr\sigma^2_f$
Rep * Fam (Prov)	pr (f-1)	MS_5	$\sigma^2_\varepsilon + n\sigma^2_{r*f(p)}$
Within plot	prf (n-1)	MS_6	σ^2_ε

Where:

- r = number of replicates
- p = number of provenances
- f = number of families per provenance
- n = number of trees per plot
- σ^2_ε = within plot variance (sampling error)
- $\sigma^2_{r*f(p)}$ = plot variance
- σ^2_f = family within provenance variance
- σ^2_{rp} = replication x provenance variance
- σ^2_p = provenance variance
- σ^2_r = replication variance

4.3.6 F-test calculations

F-Statistics were calculated to determine whether the provenance term was significant for basic wood density and pulp yield. For each F-test calculated, the null hypothesis (H_o) stated there were no significant differences between the provenance means for basic wood density and pulp yield, respectively. The alternative hypothesis (H_a) stated that at least one of the provenance means differed significantly from the rest. To test if the provenance term was significant, Satterthwaite's quasi-F ratio was used, as suggested by Steel and Torrie (1980, p. 357), and is shown below.

F ratio for the provenance term is:

$$F_{p,q} = \frac{MS_2 + MS_5}{MS_3 + MS_4} \quad \text{.....[11]}$$

where p & q are the effective degrees of freedom to be used in testing the calculated F ratio. The formulas used to calculate these two effective degrees of freedom are shown below.

$$p = \frac{(MS_2 + MS_5)^2}{\frac{(MS_2)^2}{(p-1)} + \frac{(MS_5)^2}{pr(f-1)}} \quad \text{.....[12]}$$

and

$$q = \frac{(MS_3 + MS_4)^2}{\frac{(MS_3)^2}{(r-1)(p-1)} + \frac{(MS_4)^2}{p(f-1)}} \quad \text{.....[13]}$$

4.3.7 Variance component calculations

The calculation of variance components is an important step in determining genetic parameters such as heritability, genetic and phenotypic correlations as well as predicted genetic gains. The objective here is to partition the variation found in the analysis into components attributable to different causes.

As mentioned earlier, ANOVA was conducted using the General Linear Model procedure of SAS®, where variance components were estimated using TYPE III output. Variance components due to replications (σ^2_r), provenances (σ^2_p), replication x provenance interaction (σ^2_{rp}), families (σ^2_f), replication x family within provenance interaction ($\sigma^2_{r*f(p)}$) and within-plot error (σ^2_ε) were calculated from the expectations of mean squares as indicated in Table 4.4.

Table 4.4. Components of variance calculation

Variance component	Symbol	Method of calculation
Replications	σ^2_r	$(MS_1 – MS_3) / npf$
Provenances	σ^2_p	$(MS_2 – MS_3 – MS_4 + MS_5) / nrf$
Rep x Prov interaction	σ^2_{rp}	$(MS_3 – MS_5) / nf$
Families	σ^2_f	$(MS_4 – MS_5) / nr$
Rep x Fam (Prov) interaction	$\sigma^2_{r*f(p)}$	$(MS_5 – MS_6) / n$
Within-Plot error	σ^2_ε	MS_6

where:

- r = number of replicates
- p = number of provenances
- f = number of families per provenance
- n = number of trees per plot

It is important to note, as mentioned earlier, that when variance components are estimated on a single-site basis, family-by-environment interaction variances cannot be estimated, and in fact they are added to the estimate of family variance (σ^2_f) on that particular site. Thus, the estimate of variance among families includes both σ^2_f and σ^2_{fe}, and has been referred to as biased since it does not only estimate σ^2_f (Comstock and Moll, 1963). The implication of this biased effect is that later calculations of single-site heritabilities will be inflated due to the presence of family-by-environment interaction variance within family variance (White and Hodge, 1990).

4.3.8 Narrow-sense heritability estimates

From the breakdown of the total variation into its different components (as done in the previous section), it is possible to calculate the phenotypic variance within-provenance (σ^2_T) as follows:

$$\sigma^2_T = \sigma^2_f + \sigma^2_{r*f(p)} + \sigma^2_\varepsilon \quad \text{.....[14]}$$

where:

- σ^2_f = variance due to the random effect of the l^{th} family in the k^{th} provenance
- $\sigma^2_{r*f(p)}$ = variance due to the random interaction effect of the j^{th} replication with the l^{th} family within the k^{th} provenance
- σ^2_ε = variance due to the random error term associated with the $jklm^{th}$ tree

From this, single-site (biased) narrow-sense heritability estimates within provenance (h^2) were estimated for basic wood density and pulp yield, using the following formula:

$$h^2 = (2.5*\sigma^2_f) / \sigma^2_T \quad \text{.....[15]}$$

A coefficient of 2.5 instead of 4 was multiplied with the family variance to give an estimate of the additive genetic variance. The choice of the coefficient of 2.5 in the calculation of heritability is commonly used by many authors working with *Eucalyptus* (Volker *et al*., 1994), and assumes an average rate of out-crossing of 70% for *Eucalyptus* species (Morgan and Bell, 1983; Griffin and Cotterill, 1988).

Standard errors for the narrow-sense heritability estimates were calculated according to Becker (1985), as:

$$\sigma_{(h^2)} = 2.5 * \sqrt{[2 * (1 - t)^2 * (1 + (k - 1) * t)^2] / [k * (k - 1) * (s - 1)]} \quad \text{.....[16]}$$

Where:

- k = number of offspring per family
- s = number of families
- $t = h^2 / 2.5$

4.4 Results

Results from single-site analysis of variance for basic wood density and pulp yield are presented in Tables 4.5 and 4.6, respectively. Together with this is a summary of the hypothesis tests that investigated the provenance effect for basic wood density and pulp yield, presented in Table 4.7.

Table 4.5. Single-site analysis of variance for basic wood density

Source of variation	**DF**	**SS**	**MS**	**F**	**Prob.** [a]
Replicate	4	2694.4198	673.6049	0.52	0.7229 ns
Provenance	10	82478.0992	8247.8099	6.34	<.0001 **
Rep * Provenance	40	52012.5988	1300.3150	1.14	0.3095 ns
Family (Provenance)	19	63874.2221	3361.8012	2.95	0.0005 **
Rep * Fam(Provenance)	72	82118.9426	1140.5409	1.15	0.2302 ns
Error	154	152203.0000	988.3312		
Total	299	468586.5967			

a: ns = not significant if prob. > 0.05; * = significant if prob. < 0.05; ** = highly significant if prob. < 0.01

Table 4.6. Single-site analysis of variance for pulp yield

Source of variation	df	SS	MS	F	Prob. [a]
Replicate	4	22.3552	5.5888	0.42	0.7958 ns
Provenance	10	446.3805	44.6381	3.33	0.0032 **
Rep * Provenance	40	536.8421	13.4211	1.43	0.0990 ns
Family (Provenance)	18	231.7963	12.8776	1.37	0.1777 ns
Rep * Fam(Provenance)	67	630.9894	9.4178	1.02	0.4588 ns
Error	145	1343.5375	9.2658		
Total	284	3244.1318			

a: ns = not significant if prob. > 0.05; * = significant if prob. < 0.05; ** = highly significant if prob. < 0.01

Table 4.7. Summary of hypothesis tests that investigated provenance effect for basic wood density and pulp yield

Trait	$F_{calc.}$	$F_{tab.}$	$F_{calc.} > F_{tab}$?	Accept / reject H_o?
Basic wood density	2.01	1.79	Yes	Reject H_0 and accept H_a
Pulp yield	2.06	1.75	Yes	Reject H_0 and accept H_a

H_o: $\mu_1 = \mu_2 = \mu_3 = \ldots = \mu_i$

H_a: At least one of the provenances differs significantly from the rest

p = 0.05

From the above analysis of variance of basic wood density and pulp yield, together with the hypothesis tests for the effect of provenances, it appears that for this *E. urophylla* breeding population, there are significant differences between the provenances for these

two traits, when measured at an age of 54 mo. Tables 4.8 and 4.9 indicate the mean provenance performance of basic wood density and pulp yield, respectively.

Table 4.8. Mean provenance results for basic wood density ($kg.m^{-3}$)

Provenance	**Basic wood density (± s.e.) ($kg.m^{-3}$)**	**Number of observations**	**Waller grouping [a]**
Lere-Baukrenget	520.76 (± 33.49)	70	A
La Cascada Colombia	506.40 (± 34.11)	10	A B
Mainang	505.00 (± 32.99)	30	A B
Hokeng	502.75 (± 37.83)	20	A B C
Naususu	493.25 (± 30.41)	20	B C
Lelobatan	493.15 (± 29.66)	20	B C
Ille Nggele	492.87 (± 37.40)	60	B C
Mondi bulk	484.20 (± 26.51)	10	C D
Tune	470.35 (± 45.07)	30	D E
Tutem	462.40 (± 32.70)	10	E
Kilawer	461.47 (± 37.51)	30	E

a = Provenances without common letters are significantly different at the 95% significant level

Table 4.9. Mean provenance results for pulp yield (%)

Provenance	Pulp yield (± s.e.) (%)	Number of observations	Waller grouping [a]
Lelobatan	47.60 (± 3.00)	20	A
Kilawer	46.22 (± 3.15)	20	A B
Mondi bulk	45.84 (± 2.92)	10	A B C
Mainang	45.03 (± 2.56)	28	B C D
Lere-Baukrenget	44.76 (± 3.16)	70	B C D
Ille Nggele	44.63 (± 3.19)	60	B C D
Naususu	44.02 (± 2.84)	20	C D
La Cascada Colombia	43.78 (± 4.80)	9	D
Tune	43.59 (± 3.31)	20	D E
Tutem	43.31 (± 3.70)	10	D E
Hokeng	41.69 (± 3.56)	18	E

a = Provenances without common letters are significantly different at the 95% significant level

The partitioning of the total phenotypic variances for the traits basic wood density and pulp yield into their various components are presented in Table 4.10. Variance components were calculated from the expected mean squares derived from the analysis of variance.

Table 4.10. Components of variation for basic wood density and pulp yield

Trait	Components of variation [a]					
	Provenance	Families	Rep x Provenance	Rep x Fam(Prov.)	Replications	Within – plot error
Wood density	323.1 (18.6)	279.4 (16.0)	54.6 (3.1)	95.7 (5.5)	0.0 (0.0)	988.3 (56.8)
Pulp yield	1.975 (15.0)	0.441 (3.3)	1.425 (10.8)	0.097 (0.7)	0.000 (0.0)	9.266 (70.2)

a = Percentage in parenthesis

The within-provenance phenotypic variance for basic wood density and pulp yield was calculated from the breakdown of the total variation into its different components, as shown in Table 4.10. From this, single-site (biased) narrow-sense heritability was estimated for basic wood density and pulp yield. The within-provenance phenotypic variance as well as the within-provenance heritability for basic wood density and pulp yield is presented in Table 4.11. Standard errors for the narrow-sense heritability estimates are also included.

Table 4.11. Within-provenance phenotypic variance as well as within-provenance heritability (±s.e.) for basic wood density and pulp yield at an age of 54 mo

Trait	Within – provenance phenotypic variance	Within – provenance heritability (± s.e.)
Basic wood density	1363.46	0.51 (± 0.16)
Pulp yield	9.80	0.11 (± 0.09)

4.5 Discussion

From the analysis of variance, it is clear that for this *E. urophylla* breeding population, there are significant differences between the provenances for basic wood density and pulp yield. These results identified those provenances that produced the highest basic wood density and pulp yield. The results show that in this breeding population, the provenances Lere-Baukrenget, La Cascada Colombia and Mainang consistently produced the highest values for basic wood density, whereas Tune, Tutem and Kilawer produced the weakest performance for basic wood density. For pulp yield, provenances Lelobatan and Kilawer produced the highest yields, whilst Tune, Tutem and Hokeng produced the poorest pulp yield figures.

For both basic wood density and pulp yield, within-plot variation was a major source of variation (56.8% and 70.2%, respectively). This variation pattern is not uncommon in genetic tests of forest tree species. The ratio of variance of additive genotypic effects to the phenotypic effects for basic wood density was generally high, showing strong additive genetic effects in the total variability for basic wood density in this population. However, for pulp yield, the ratio was generally weak, therefore showing the potential importance of non-additive genetic effects in the total variation for pulp yield in this population. Another observation made was that the effect of replicates was virtually zero and is indicative of a homogeneous test site. Replicate-by-provenance and replicate-by-family within provenance interactions were not statistically significant for basic wood density. Further were these variance components were small when compared to variance due to provenances and families. For pulp yield, the replicate-by-family within

provenance component of variation was not significant. However, although the variation due to replicate-by-provenance interaction was also not significant, it did outweigh the component of variation due to families. As was the case of basic wood density, the variation in pulp yield due to provenances remained a very strong component of variation.

Narrow-sense heritability for basic wood density was found to be strong whilst for pulp yield it was moderate to weak. The strong heritability for basic wood density in this breeding population provides an opportunity to make substantial gains in this trait. Although the heritability for pulp yield in this breeding population was found to be moderate to weak, this still gives tree breeders the opportunity to make significant gains through accurate selection in this *E. urophylla* population. The heritability values found here for basic wood density compare favorably to heritability estimates from another *E. urophylla* experiment conducted by Jianzhong (2003). However, they were lower for heritabilities of the same trait in the same species as found by Brasil and Veiga (1994) as well as Wei and Borralho (1997). The over-all trend of high heritabilities for basic wood density in *E. urophylla* was confirmed in this study. Although no heritability estimates of pulp yield for *E. urophylla* could be found in the literature, heritability studies for pulp yield on other *Eucalyptus* species have shown higher heritability values than those determined in this study (Matheson *et al*., 1986; Tibbits and Hodge, 1998; Raymond *et al*., 2001; Apiolaza *et al*., 2005).

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CHAPTER 5. GENETIC CORRELATIONS BETWEEN GROWTH, BASIC WOOD DENSITY AND PULP YIELD

5.1 Abstract

300 individually sampled trees were collected from a *Eucalyptus urophylla* S.T. Blake provenance/progeny trial in KwaZulu-Natal to measure the genetic and phenotypic associations that may exist between volume growth, basic wood density and pulp yield.

The genetic correlation between volume growth and pulp yield was positive and moderately strong (r_A = 0.66). This moderately strong association between volume growth and pulp yield also produced the smallest standard error (s.e. = ± 0.17). The genetic correlation estimate between volume growth and basic wood density was found to be negative but weak (r_A = -0.08). The genetic association between pulp yield and basic wood density was found to be positive but weak (r_A = 0.17). Both genetic correlation estimates between volume growth and basic wood density, as well as between pulp yield and basic wood density produced standard errors greater that the correlation itself (s.e. = ± 0.32 and ± 0.22, respectively). These high standard errors coupled with weak genetic correlations would suggest that these correlation estimates appear to be non-significant. However, these correlation estimates have a value in making breeding choices, if treated with caution.

In order to increase the accuracy of these correlation estimates, it is suggested that the sample sizes need to be increased. For future assessments of genetic correlations

between growth, basic wood density and pulp yield, it is proposed that a sampling and screening strategy should be implemented that would allow for bigger sample sizes to be measured. Such an alternative to traditional sampling and assessment protocol would require non-destructive sampling coupled with near-infrared reflectance analysis (NIRA).

Due to the type and magnitude of additive genetic correlations observed between the three traits investigated in this test, selection for any one of the three traits alone will most probably have an adverse effect on the other two. Future selections to be made in this *E. urophylla* breeding population would therefore have to incorporate a multiple trait index selection strategy, where all three traits would have to be weighed into one index value.

Key words: *Eucalyptus urophylla*, genetic correlation, volume growth, basic wood density, pulp yield, non-destructive sampling, near-infrared analysis, multiple trait index selection

5.2 Introduction

Eucalyptus urophylla S.T. Blake has become increasingly important for wood production in low altitude South African plantations where trees are grown in seasonally dry, tropical to subtropical climates. In South Africa, *E. urophylla* is predominantly used as a hybrid partner with *Eucalyptus grandis* Hill ex Maiden. This hybrid combination (GU) plays an important role in producing raw material for the Kraft pulping industry in the country.

Wood properties are widely recognized as being important to end-product value and overall profitability in pulp production (Kube *et al*. 2001). Relationships between wood properties and profitability of Kraft pulping are well documented (Dean *et al*. 1990; Borralho *et al*. 1993; Greaves *et al*. 1997). Studies have found that an increase in basic wood density and pulp yield is important for Kraft mill productivity (Kube *et al*. 2001). From the point of view of plantation production, high basic wood density combined with high volume growth maximizes production on the land unit area where trees are grown (Miranda *et al*. 2001).

Despite the increasingly important role that *E. urophylla* plays in South African commercial plantation forestry, basic information on the genetic and phenotypic correlations between growth, basic wood density and pulp yield found in the species when grown in this country, is not well known. This basic information is essential in determining optimum breeding strategies for the species (Borralho *et al*. 1992). The aim of this chapter was to provide estimates of additive genetic and phenotypic associations

that may exist between these three important traits, and to provide some discussion on how these associations may have an impact on the breeding strategy implemented.

5.3 Materials and methods

5.3.1 Genetic material

During 1999, a field trial of open-pollinated *E. urophylla* provenance/progeny seed lots was established in northern KwaZulu-Natal, South Africa. Although the test included 306 half-sib families, representing a total of 17 different provenances, data from only 30 families were used to study the genetic and phenotypic associations that existed between growth, basic wood density and pulp yield. Information on the families used in this study is provided in Table 5.1. The 30 families used in this study were selected on the basis of their superior growth performance shown in the greater breeding population.

Table 5.1. Family information represented by provenances in the study

Provenance name	**Latitude (S)**	**Longitude (E)**	**Altitude range (m)**	**Family number**
Hokeng	8° 31’	122° 47’	350-800	371
				387
Ille Nggele	8° 39’	122° 26’	610-800	300
				306
				307
				311
				316
				317
Kilawair	8° 41’	122° 29’	225-530	342
				353
				358
La Cascada Colombia	---	---	---	995

Table 5.1 continued

Provenance name	Latitude (S)	Longitude (E)	Altitude range (m)	Family number
Lere-Baukrenget	8° 39’	122° 23’	700-750	323
				324
				330
				331
				332
				336
				337
LelobatanI	9° 41’	124° 14’	1200-1400	409
				417
Mainang	8° 14’	124° 39’	1100-1250	221
				225
				235
Mondi bulk	---	---	---	902
Naususu	9° 38’	124° 13’	1200-1450	128
				131
Tune	9° 33’	124° 19’	1100-1400	181
				191
Tutem	9° 35’	124° 17’	1200-1400	164

5.3.2 Test site information

The site selected for the field trial represents a typical target environment for *E. grandis x E. urophylla* (GU) hybrid clonal plantations in South Africa. Such an environment is typically in humid, tropical to sub-tropical, summer rainfall areas, with very little or zero frost, extended dry periods during winter and deep, well-drained soils. Table 5.2 provides location and climatic information of the site utilized in this study.

Table 5.2. Location and climatic conditions of *Eucalyptus urophylla* provenance/progeny field trial

Map Key[1]	Geographic location	Mondi farm	Latitude (S)	Longitude (E)	Altitude (m)	MAP (mm)	MAT (°C)
1	Northern KwaZulu Natal	Flatcrown	28° 33’	32° 07’	71	1008	21.6

1 = key to field trial location in Figure 5.1; MAP = mean annual precipitation; MAT = mean annual temperature.

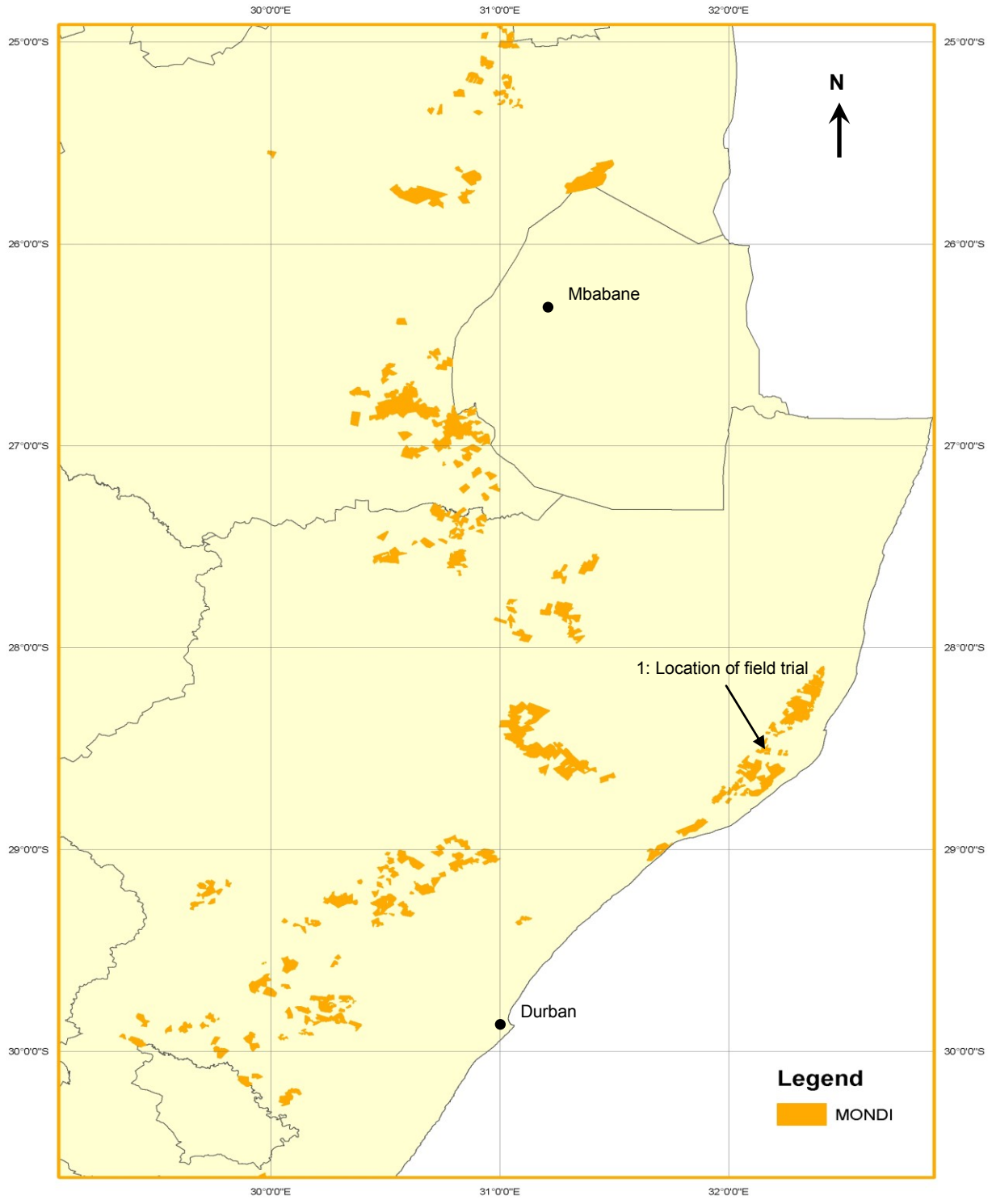

Figure 5.1 Location of field trial

5.3.3 Field trial design

The original trial design was a randomized complete block with five replicates and 1 x 6 tree row plots. Within each replicate, families from the same provenance were randomly blocked together, with each provenance block randomly distributed across the five replicates.

Trees were established at a 3m x 2m espacement, giving a total of 1667 trees per hectare. Silviculture treatments such as pre-plant site preparation, planting, fertilizer application and weeding were all done to similar commercial standards as required by Mondi plc. The design, in-field layout and silviculture treatments were all applied in such a manner to reduce the environmental variation between trees to a minimum.

5.3.4 Data collection

5.3.4.1 Growth traits

The first sets of data collected for this study were tree height and diameter. Data was collected from all trees at an age of 48 mo. Total tree height (HT) was measured with a Vertex® hypsometer. Diameter at breast height (DBH) was measured with a diameter tape. Individual tree volumes were estimated by using the following volume equation developed for *Eucalyptus* seedlings by the Forest Technical Department of Mondi.

Individual Tree Volume (m^3) = (3.1415927/40000).k.DBH^2.HT ……[**17**]

Where k = (B/3)+(A/2)-(A+B)+((C/3).E)+((D/3).F)

And A = -2.55302 D = 228.6886

B = 1.115693 E = 0.583127

C = -0.75464 F = 0.000068

5.3.4.2 Wood and fiber traits

The collection of wood samples was done when the trees were 54 mo old. Each of the 30 families used in this study had 10 trees randomly sampled in order to screen the provenances and families for basic wood density and pulp yield performance.

Collection of wood samples for this study was done on a destructive basis by felling the selected trees, after which wood disks were removed. Whole disks were removed from each tree, starting at the base of the tree and thereafter at every 1m interval up the length of the tree, until a top diameter of 50mm was reached. At every 1m interval, including the base-cut, two 20mm thick disks were removed. The first disk of each cut-interval was used to screen basic wood density, while the second disk was used to screen pulp yield. All the disks sampled per tree for basic wood density was bagged together so that a cone-shaped sample was available for screening. The same bagging process was followed to collect material for screening of pulp yield. An example of such cone-shaped samples is provided in Figure 5.2.

Figure 5.2. Cone-shaped samples collected from an individual tree to screen for basic wood density and pulp yield.

Basic wood density is defined as oven-dry wood mass per unit volume of green wood (Kube and Raymond, 2002). Volumes of the green (water-saturated) samples were measured using the water displacement method, and the oven-dry weight of each sample was then determined after drying at 105°C for 10 hours. The volumes and oven-dry weights were used in the following model to determine basic wood density.

$$D = (W / V) * 1000 \quad \text{.....[18]}$$

Where:

- D = basic wood density ($kg.m^{-3}$)
- W = oven-dry weight of the sample (g)
- V = volume of the water-saturated sample (ml^3)

Pulp yield is defined as the proportion of dry mass recovered as pulp to the total dry mass of wood used in the pulping process (Beadle *et al*. 1996). Kraft pulping involves cooking wood chips in an alkaline solution at an elevated temperature and pressure to dissolve lignin, leaving intact fibers that are composed of cellulose and hemicelluloses (Smook, 1982).

For this study, the disks selected for the screening of pulp yield were chipped using a laboratory guillotine chipper. All wood chips derived from the disks of the same tree were mixed. This allowed selection of a composite sample of wood chips that were a true representation of the whole tree. Each tree was individually pulped in a rotating Aurora laboratory digester. Figure 5.3 presents a photograph of such a digester used in this study.

The resultant pulp from this cooking process was screened using a Packer screen with 0.8mm slots. Pulp yield was calculated as a percentage of the oven-dry mass of wood used to charge the digester.

Figure 5.3. Rotating Aurora laboratory digester used in this study to pulp wood chips.

The wood chip samples were pulped under the following conditions:

- 1000g of oven-dry wood
- 15% active alkali as NaOH based on the oven-dry wood
- Kraft cooking liquor with a Sulphidity of 25%
- Liquor to wood ratio of 4.6 : 1
- Pulping temperature of 170°C
- Ambient to 170°C in 90 minutes
- Degassing at 90°C and 105°C
- H-factor of 900

5.3.5 Additive genetic and phenotypic correlation estimates

Additive genetic (r_A) and phenotypic (r_P) correlations were estimated using individual tree data. Analysis was conducted using the General Linear Model procedure of SAS®, where variance and covariance components were estimated using TYPE III output. The following linear model was used for data analysis.

$$Y_{jkl} = \mu + r_j + f_k + (r*f)_{jk} + \varepsilon_{jkl} \quad \text{.....[19]}$$

Where:

- Y_{jkl} = phenotypic observation from the jkl^{th} tree
- μ = overall mean in the test
- r_j = random effect of the j^{th} replicate within the test; $E(r_j) = 0$ and $Var(r_j) = \sigma^2_r$
- f_k = random effect of the k^{th} family; $E(f_k) = 0$ and $Var(f_k) = \sigma^2_f$
- $(r*f)_{jk}$ = random effect due to interaction of the j^{th} replicate with the k^{th} family; $E((r*f)_{jk}) = 0$ and $Var((r*f)_{jk}) = \sigma^2_{rf}$
- ε_{jkl} = random error term associated with the jkl^{th} tree; $E(\varepsilon_{jkl}) = 0$ and $Var(\varepsilon_{jkl}) = \sigma^2_\varepsilon$

In order to remove scale effects and help to create homogeneous variance structures across replicates, the square root of the replicate phenotypic variance was used to standardize all traits before analysis (Falconer, 1993; White, 1996; Osorio *et al*. 2003). That is, for each trait, each tree's measurement was divided by the phenotypic standard deviation of its corresponding replicate, producing a transformed variable with a phenotypic variance of one (Osorio *et al*. 2003).

Single-site additive genetic correlations between the traits (Type A, Burdon, 1977) were calculated using an auxiliary variable (X + Y) for each pair of traits X and Y. Since Var (X + Y) = Var (X) + Var (Y) + 2Cov (X, Y), the variance components associated with these auxiliary variables can be decomposed into variance due to X, variance due to Y, and the covariance of X and Y (Kempthorne, 1957). Whilst this method is old, it does work well (Searle *et al*. 1992).

Analysis for total phenotypic variance of the auxiliary variables, and subsequent partitioning of this variance into components due to family effect (σ^2_f), replicate by family within provenance interaction effect ($\sigma^2_{r*f(p)}$) and error (σ^2_ε) were conducted using the General Linear Model Procedure of SAS®. Variance components were estimated using Type III output.

The family covariance component ($\sigma_{fx,y}$) was used to estimate the single-site additive genetic correlation (r_A) as follows:

$$r_A = \sigma_{fx,y} / (\sigma^2_{fx} * \sigma^2_{fy})^{0.5} \quad \text{.....[20]}$$

Where $\sigma_{fx,y}$ is the estimated family covariance between traits X and Y, and σ^2_{fx} and σ^2_{fy} the estimated family variances of traits X and Y respectively.

$\sigma_{fx,y}$ was calculated from:

$$\sigma_{fx,y} = (\sigma^2_{fx+y} - \sigma^2_{fx} - \sigma^2_{fy}) / 2 \quad \text{.....[21]}$$

Where σ^2_{fx+y} is the estimated family variance of the auxiliary variable (X + Y).

Standard errors of genetic correlations were approximated using Robertson's (1959) equation as:

$$\sigma_{rA} = \left\{ \frac{(1 - r_A^2)}{(2)^{0.5}} \right\} * \left\{ \frac{\sigma_h^2{}_x * \sigma_h^2{}_y}{h^2_x * h^2_y} \right\}^{0.5} \quad \text{.....[22]}$$

Where r_A is the genetic correlation and σ_h^2 is the standard error of the heritability.

For the calculation of phenotypic correlations, the Pearson product-moment correlation coefficient (r_P) was computed as:

$$r_P = \frac{\text{Cov (X, Y)}}{\text{Std (X) * Std (Y)}} \quad \text{.....[23]}$$

Where Cov (X, Y) is the phenotypic covariance between traits X and Y; Std (X) and Std (Y) are the phenotypic standard deviations of characters X and Y, respectively.

5.4 Results

Additive genetic correlations (r_A), together with their standard errors are presented above the diagonal line in Table 5.3. Phenotypic correlations (r_P) between the traits are presented below the diagonal line.

Table 5.3. Additive genetic correlations (± s.e.), and phenotypic correlations between traits investigated

	VOL	**PY**	**WD**
VOL		0.66 (± 0.17)	-0.08 (± 0.32)
PY	0.02		0.17 (± 0.22)
WD	-0.16	0.04	

VOL = Volume growth; PY = Pulp yield; WD = Basic wood density

The genetic correlation observed between volume growth and pulp yield was positive and moderately strong (r_A = 0.66). For the three different trait combinations investigated, the association between volume growth and pulp yield was the strongest. This moderately strong association between volume growth and pulp yield also produced the smallest standard error (s.e. = ± 0.17) for the correlation coefficient observed. The phenotypic correlation observed between volume growth and pulp yield was weaker than the genetic correlation observed between the same two traits (r_P = 0.02).

The genetic and phenotypic correlation estimates between volume growth and basic wood density were found to be negative. However, although genetic and phenotypic associations were negative, both were found to be weak (r_A = -0.08; r_P = -0.16). Further

was it also found that the standard error of the genetic correlation between volume growth and basic wood density to be bigger than the correlation estimate (s.e. = ± 0.32).

Genetic and phenotypic associations between pulp yield and basic wood density were found to be positive but weak, especially the phenotypic association (r_A = 0.17; r_P = 0.04). Also was it found that the standard error of the genetic correlation between pulp yield and basic wood density was bigger than the correlation estimate itself (s.e. = ± 0.22).

5.5 Discussion

There appears to be favorable genetic correlations between volume growth and pulp yield (r_A = 0.66), and although weak, between pulp yield and basic wood density (r_A = 0.17). A weaker, negative genetic correlation was observed between volume growth and basic wood density (r_A = -0.08).

It seems that substantial improvements can be made in volume growth and pulp yield using straightforward breeding procedures such as individual tree selection based on only one of the two traits. However, given that the correlation is only moderate in strength, and coupled with a relatively high standard error (s.e. = ± 0.17), the danger does exist that the tree breeder may dilute one of the traits when only selecting for the other. For a scenario such as this, it is therefore proposed that tree breeders should make broad selections based on family, and where possible, provenance data for

volume growth, whereafter measurements must be made of pulp yield within families and provenances in order to select suitable breeding parents for both traits.

The standard errors of the genetic correlations between volume growth and basic wood density, as well as between pulp yield and basic wood density, (± 0.32 and ± 0.22, respectively), were both greater than the actual genetic correlations observed, indicating that these correlations must be interpreted with caution. These high standard errors coupled with weak genetic correlations would suggest that these correlation estimates are probably non-significantly different from zero. Standard errors higher than the correlation estimates suggest that a more precise method is required to quantify these traits (Valencia-Manzo and Vargas-Hernandez, 2001). Small sample sizes remain an issue for the estimation of genetic parameters, especially genetic correlations (Apiolaza *et al*. 2005).

The sizes of the samples used in this study to measure genetic and phenotypic associations between the three traits were indeed small. This is a result of the type of sampling and measurement techniques implemented in this study. Traditionally, destructive sampling of trees, as well as assessment of Kraft pulp yield by cooking wood chips to a fixed kappa number in a laboratory digester is slow and expensive, thereby restricting the number of samples that may be processed. For assessing the quality of a plantation resource, or evaluating silvicultural or genetic effects on wood quality, large numbers of samples need to be processed (Raymond and Schimleck, 2002). An alternative to the traditional sampling and assessment method of Kraft pulp yield is to

make use of near-infrared reflectance analysis (NIRA) as prescribed by Michell (1995), and Schimleck and Michell (1998). NIRA involves measuring the spectra of a large number of samples whose Kraft pulp yield is known, developing a model that relates the near-infrared spectra of each sample to its pulp yield at the desired kappa number and then using the model to predict the pulp yield for a new sample from this near-infrared spectra (Raymond *et al*. 2001). NIRA is potentially of value in tree breeding programs because the quantity of wood required is very small (± 3g air-dry), allowing the prediction of pulp yield from small wood samples, such as increment cores (Raymond *et al*. 2001). The removal of increment cores from trees are quick and non-destructive, allowing for much larger samples to be collected in order to evaluate pulp yield. This increase in sample size will improve the accuracy of genetic correlation estimates by reducing the standard error of the calculated correlation estimates.

Due to the type and magnitude of additive genetic correlations observed between the three traits investigated in this test, selection on any one of the three traits alone may have an adverse effect on the other two. Future selections to be made in this *E. urophylla* breeding population would therefore have to incorporate a multiple trait index selection strategy, where all three traits will have to be weighed into one index value.

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CHAPTER 6. OVERVIEW

6.1 Introduction

This study used quantitative analysis to investigate the genetic variance of, as well as genetic correlations between, volume growth, basic wood density and pulp yield. Data was collected from a provenance/progeny trial of *Eucalyptus urophylla* S.T. Blake, planted on the KwaZulu-Natal coastal plain of South Africa.

The study determined whether there were any significant genetic differences between the various provenances for volume growth, basic wood density and pulp yield. The study also estimated the levels of additive genetic control over each of the three traits measured. Finally, the study provided estimates of additive and phenotypic associations that existed between volume growth, basic wood density and pulp yield.

This information is of critical importance because it broadens the limited knowledge base of *Eucalyptus urophylla* grown in South Africa, and also provides essential information needed in a tree improvement program aiming to deliver trees that will produce maximum yields of fiber in a Kraft pulping process.

6.2 Principal findings

Principal findings of this study are summarized as follows:

6.2.1 Growth traits (Chapter 3)

a. Highly significant differences were observed between provenances, as well as between families within provenances for diameter, height and volume growth. The results identified Watakika, Mainang and Apui as provenances that produced the best growth rates.
b. The ratios of variance of additive genotypic effects to the phenotypic effects were generally weak for all three growth traits. This identified the potential importance of non-additive genetic effects in the total variability of the growth traits measured in this population.
c. The environmental effect of replicates was virtually zero and is indicative of a homogeneous test site. Although replicate-by-provenance and replicate-by-family within provenance interactions were statistically significant for all three growth traits, their variance components were found to be small when compared to variance due to provenances and families.
d. Although narrow-sense heritabilities for all three growth traits were found to be moderate to weak, it still provided the opportunity to make significant genetic gains through accurate selection.

6.2.2 Wood and fiber traits (Chapter 4)

a. Significant provenance effects were observed for both basic wood density and pulp yield. Provenances Lere-Baukrenget, Mainang and Hokeng produced the highest values for basic wood density, whilst Provenances Lelobatan and Kilawer delivered the highest values for pulp yield.

b. The ratio of variance of additive genotypic effects to the phenotypic effects for basic wood density was generally high, showing strong additive genetic effects in the total variation for basic wood density. However, for pulp yield, the ratio was generally weak, therefore showing the potential importance of non-additive genetic effects in the total variation for pulp yield.

c. Replicate-by-provenance and replicate-by-family within provenance interactions were not statistically significant for basic wood density. These variance components were small when compared to variance due to provenances and families. For pulp yield, the replicate-by-family within provenance component of variation was not significant. However, although the variation due to replicate-by-provenance interaction was also not significant, it outweighed the component of variation due to families. As was the case with basic wood density, the variation in pulp yield due to provenances remained a very strong component of variation.

d. Narrow-sense heritability for basic wood density was found to be strong whilst narrow-sense heritability for pulp yield was moderate to weak. This suggests that big genetic gains can be achieved for basic wood density, and through accurate selection, significant gains for pulp yield.

6.2.3 Genetic correlations between growth, basic wood density and pulp yield (Chapter 5)

a. The genetic correlation between volume growth and pulp yield was positive and moderately strong. This correlation also produced the smallest standard error. A positive but weak genetic correlation existed between pulp yield and basic wood density. A negative but weak genetic correlation was observed between volume growth and basic wood density.
b. The standard errors of the genetic correlations between volume growth and basic wood density, as well as between pulp yield and basic wood density, were both greater than the actual genetic correlations observed, indicating that these two correlations must be interpreted with caution.
c. The sizes of the samples used in this correlation study were too small and had a negative effect on the results when analyzing the data.

6.3 Principal conclusions

Principal conclusions of this study are summarized as follows:

a. The trial produced adequate data that will allow the tree breeder to distinguish between better and weaker performing provenances for growth, basic wood density and pulp yield. This breeding population also exhibited adequate genetic control over the three traits that will allow for genetic improvement through selection.

b. Correlation estimates appear to be non-significant as suggested by weak genetic correlations coupled with high standard errors. However, these genetic correlations were estimated from relatively small sample sizes, and must therefore be treated with caution since they are used to determine the type of selection strategy to be implemented and subsequently, used to determine genetic gains achieved in each of these important traits.

6.4 Future work

Recommendations for future work in this field are summarized as follows:

a. Investigation of genotype x environment interactions (GxE) that may exist for economically important traits of this species. Determining the size and practical importance of GxE is critical for designing tree breeding programs and making decisions about plantation establishment (Muneri and Raymond, 2000).
b. Quick, cheap and non-destructive wood sampling strategies coupled with rapid screening equipment and protocols need to be implemented in order to screen much larger sample sizes of wood. This will improve genetic correlation estimates between different traits.
c. With sound knowledge on GxE and genetic correlations, the implication of these genetic parameters needs to be examined in terms of genetic gains expected from selection.

6.5 Reference

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