

## Abstract

**Stanger, Terence Keith.** Variation and Genetic Control of Wood Properties in the Juvenile Core of *Pinus patula* Grown in South Africa. Under the direction of William S. Dvorak and Gary R. Hodge.

*Pinus patula* is a closed-cone pine that has a rather narrow, but long, distribution in Mexico. It ranges from approximately 16°N to 24°N latitude, is generally restricted to humid, sub tropical to near temperate sites, with deep, fertile clay soils, and an estimated mean annual precipitation of 1000 to 2500 mm. Approximately one million hectares of *P. patula* plantations have been established in the tropics and sub tropics for saw-timber and paper products. The majority of the *P. patula* forests are located in southern Africa with South Africa having more than 300,000 hectares under operational management. Since 1986 the CAMCORE Co-operative has sampled 25 provenances and 624 mother trees of *P. patula* in Mexico. The CAMCORE collections represent the most complete coverage of the species natural distribution to date. During December 1990, a series of five trials of open-pollinated *P. patula* family/provenance seedlots were established adjacent to each other at Maxwell in KwaZulu-Natal, South Africa. These trials are 10.5-years-old and offered a unique opportunity to sample material from the entire geographic range of the species grown on a single site.

Nine hundred and seventy-two individual trees, representing 12 provenances and 108 half-sib families were sampled non-destructively by removing 12 mm increment cores at breast height. Wood anatomical properties (wood density traits, tracheid length and tracheid cross-sectional properties) were measured using gamma ray densitometry and image analysis. The phenotypic variation in wood properties was characterized at the provenance, family and individual tree level. A strong clinal trend was shown to exist between wood property traits and latitude of collection site, with the highest correlation ( $r = 0.97$ ) with tracheid radial diameter. Provenance differences were strong and significant for most wood properties, while large

individual tree-to-tree variation existed for all wood properties. *P. patula* var. *patula* and *P. patula* var. *longipedunculata* appear to have markedly different wood.

The additive genetic control of wood properties varied from zero (for tracheid length from ring 8) to moderately strong ( $h^2 = 0.51$ ) for tracheid radial diameter. Heritability estimates for wood density traits were slightly lower than what have been reported by other authors. However, mean earlywood density, a component of overall wood density, had a much higher heritability ( $h^2 = 0.37$ ) than area weighted mean core density ( $h^2 = 0.27$ ). Contrary to most reports in the literature, the findings in this study show that tracheid length and cell wall thickness in *P. patula* are under very weak or negligible additive genetic control. Given the low level of additive genetic variation, tracheid length and cell wall thickness should not be included as a selection criteria in *P. patula* breeding programs in South Africa.

Moderate gains, ranging from one to 22 percent, are possible from direct selection on wood property traits. Predicted correlated responses show that, in some cases, indirect selection may lead to larger or equivalent responses compared to direct selection. The finding that a moderately strong negative genetic correlation ( $r_A = -0.46$ ) exists between diameter growth and wood density has important implications for applied breeding programs.

Variation and Genetic Control of Wood Properties in the  
Juvenile Core of *Pinus Patula* Grown in South Africa

By  
Terence Keith Stanger

A dissertation submitted to the Graduate Faculty of North Carolina State University  
in partial fulfilment of the requirements for the degree of  
Doctor of Philosophy

DEPARTMENT OF FORESTRY

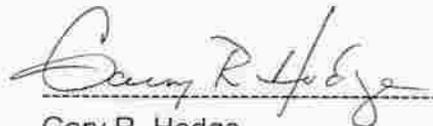
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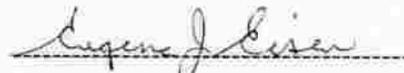
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***This thesis is dedicated to:***

***My wife Centa and two boys, Keith and Luke.***

***Ms. Kay Nixon and Dr Mike Shaw  
my mentors during my early days  
as a forestry researcher.***

## Biography

Terence Keith Stanger was born in Port Shepstone, KwaZulu-Natal, South Africa on the 29<sup>th</sup> March 1962. He attended Margate Primary School and Port Shepstone High School, matriculating in 1979. After completing two years compulsory military service in the South African Defence Force, he studied at the University of Natal, Pietermaritzburg, obtaining in 1985 a B.Sc. in Agriculture majoring in genetics.

After graduating he joined the Department of Agriculture's Maize Breeding program, based in Pietermaritzburg. After completing a year's work he started studying part time and at the end of 1988 obtained a M.Sc. in Agriculture (*cum laude*) majoring in genetics and plant breeding from the University of Natal, Pietermaritzburg. In June 1993 he joined the Institute for Commercial Forestry Research (ICFR) in Pietermaritzburg and began a career in Forestry Research.

On joining the ICFR he held the position of geneticist in a Eucalypt breeding program funded by the South African Mining Timber Manufacturers Association. While at the ICFR, he attained the position Program Manager Tree Improvement. In 1993 he left the ICFR and joined Sappi Forests Research as Program Leader: Pine Breeding. He held this position until he left for North Carolina State University in July 1999 to study towards his Ph.D. During an 18 month three semester stay in Raleigh, North Carolina, he was able to complete the course work requirements for this Ph.D. In December 2000 he returned to South Africa to complete the research component of his research which is reported on in this thesis. He currently holds the position Program Leader: Hardwood Breeding with Sappi Forests Research in South Africa.

He is married to Centa and has two boys, Keith and Luke.

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I would like to thank the CAMCORE members for their friendship and support over the years. I hope future students continue to benefit from the CAMCORE stipend that I was awarded for 18 months.

Without the financial support of Sappi, this study would not have been possible. I am indebted to them for their support and for allowing me the time to pursue and complete this project. In particular thanks must go to Andrew Morris, the General Manager of our research group, for supporting and encouraging me to undertake the project and complete it timeously. A special word of thanks must go to my colleagues at Sappi Forests Research who may have had to carry a higher than normal workload during my absence.

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## Chapter 1

### Introduction

#### 1.1 Natural habitat

*Pinus patula* is a closed-cone pine that has a rather narrow but long distribution in Mexico. It is found from approximately 16° N to 24° N latitude on humid, subtropical to near temperate sites in areas with deep, fertile clay soils. Mean annual precipitation amounts range from 1000 to 2500 mm (Perry, 1991), with additional moisture being received throughout the year in the form of heavy mists, clouds and fog. Although this pine has been found growing at elevations ranging from 1500 to 3100 m, most of the principal stands of its central distribution occur from 2100 to 2800 m altitude. The species can withstand heavy frosts (-10°C) and dry periods of 4 to 5 months but grows much better under warm, humid conditions. Within its native range, it attains heights of 30 to 35 m with diameters of 50 to 90 cm (Perry, 1991).

Two varieties of *Pinus patula* have been described, var. *patula* and var. *longipedunculata*. *Pinus patula* Schiede ex Schlecht. & Cham. var. *patula* occurs in the Sierra Madre Oriental from Tamaulipas to northeastern Oaxaca, Mexico (Dvorak *et al.*, 2000). The natural distribution of *P. patula* Schiede ex Schlecht. & Cham. var. *longipedunculata* Loock ex Martínez overlaps with var. *patula* in northeastern Oaxaca and extends westward along the Sierra Madre de Sur as far as Guerrero (Dvorak *et al.*, 2000). Both varieties are included in this study. A detailed description of the species natural distribution, the tree and the CAMCORE collection sites can be found in Dvorak *et al.* (2000) and will not be repeated here. Provenance details for the material included in this study are described in Chapter 2.

## 1.2 A plantation species in South Africa

Approximately one million hectares of *P. patula* plantations have been established in the tropics and sub-tropics for saw-timber and paper products (Birks and Barnes, 1991). The majority of the *P. patula* forests are located in southern Africa with South Africa having the largest area under operational management.

Plantation forestry in South Africa occupies 1.33 million hectares (DWAF, 2002), predominantly in the summer rainfall region along the eastern seaboard and interior of South Africa. In South Africa pine plantations are 707,205 hectares in extent, 337,000 of which are planted to *P. patula*. It is therefore the single most important commercial timber species in South Africa. Twenty four percent of the total roundwood intake by pulp, paper and board mills in South Africa is softwood (DWAF, 2002), *P. patula* makes up at least half of this intake and is the preferred species for ground-wood pulp production. Despite its importance, at the time when this study was initiated in August 2000, no detailed studies had been conducted on *P. patula* to characterize the phenotypic and genetic variation in wood properties. Other than for wood density, genetic parameter estimates were not available.

*Pinus patula* was first introduced into South Africa in 1907 (Poynton, 1977). Seed for the original introductions was obtained via intermediary seed merchants, so the exact provenances of origin are not known. It has been suggested that the likely source of the early seed collections were *P. patula* stands near Mexico City (Poynton, 1977). This would correspond to provenances from the central portion of the species natural distribution. It could be said that tree breeding programs really started in South Africa as early as 1953 when a progeny trial comprising 125 open-pollinated families, collected from various plantations in the Mpumalanga province, was established at Border plantation. However it was with the inception of the “D.R. de Wet Forest Research Station” near Sabie, that tree improvement started in earnest. Currently the two major industrial timber growers (Mondi and Sappi) in South Africa have their own

*P. patula* breeding programs, but neither routinely includes wood properties in their selection criteria.

### **1.3 Tree breeding and wood properties**

One of the disadvantages of wood, compared to other raw materials used in manufacturing industries, is its great variability. However, from a tree breeding perspective, this provides many opportunities for improvement. Zobel and Jett (1995) provide a comprehensive summary of the genetics of wood production. In general it has been reported that wood properties are under strong genetic control. This suggests that selection and breeding for these properties should be successful. Zobel and Jett (1995) state that wood improvement is most needed for pines that are grown as exotics in the tropics and sub-tropics. The advantages of exotics are rapid growth and a young harvestable age, but generally they have poor form and a high proportion of juvenile wood. Much of the recent expansion in plantation forestry is occurring in the tropics and sub-tropics where a number of new species are being tested such as *Pinus greggii*, *P. maximinoi*, and *P. tecunumanii*. In most cases, very little or nothing is known about the wood properties of these new species when they are grown as exotics in plantations.

Genetic improvement of wood quality in young, fast-grown tropical plantations may provide a solution to the high levels of juvenile wood in these plantations. Most tree improvement programs traditionally include adaptability, growth, stem form, disease and pest resistance in their assessments, but very few programs routinely include wood properties. Historically, very few studies were specifically designed to assess the genetic control of wood properties. However, by the mid 1960's it was generally accepted that the genetic control of wood properties was of significant magnitude to be included in breeding programs (Zobel and Jett, 1995).

To be used routinely in a tree breeding program, any pulpwood assessment strategy for wood properties must be convenient, cheap and rapid, and must be able to cope

with samples from thousands of trees. Evans *et al.* (1995) suggest that for routine assessment of wood properties to be effective, the following criteria must be met:

- 1) sampling is non-destructive,
- 2) sample size is small,
- 3) sampling rate is high,
- 4) measurement rate is high and repeatable,
- 5) sample properties reflect those of the whole resource and,
- 6) resource properties control product properties.

With advances in technology, the first four criteria can be accomplished, and published evidence suggests that the latter two are acceptable for pines (Evans *et al.*, 1995. Ladrach, 1984 and Blair *et al.*, 1975).

It is well recognized that patterns of wood development vary considerably between trees. However, relating the wood properties measured at limited points in the tree to the average of the whole tree offers the possibility of rapid assessment of wood properties from cores taken at a single convenient sampling point. This in particular has application in screening selected trees in a tree breeding program where relative values for ranking trees, and not absolute estimates of the whole tree wood properties, are important.

A number of authors have investigated and correlated single point sampling with whole tree properties. Ladrach (1984) developed a regression model to predict whole tree specific gravity for *P. patula* in Colombia from specific gravity determined at breast height. The age of the trees varied from four to 23 years and the  $R^2$  for the model based on a sample size of 75 trees was 0.93. Ringo and Klem (1980) have also shown that single increment cores extracted at breast height from 25-year-old *P. patula* grown in Tanzania can be used to estimate whole tree basic density. Their results showed that wood density determined using increment cores, underestimate whole tree values by about 4%. Wheeler *et al.* (1966) demonstrated a definite

relationship ( $r = 0.88$ ) between dimensions of sample tracheids taken at the 5 foot height level and whole tree tracheid length and tangential diameters for loblolly pine. This study demonstrated the utility of breast height sampling of tracheid lengths and tangential diameters for comparing these characteristics between trees (Wheeler *et al.*, 1966). Ladrach (1984) also showed for *P. patula* that tracheid length of the entire tree correlates well with samples taken at breast height ( $R^2 = 0.96$ ). Sufficient evidence is available in the literature to support single point, non-destructive sampling in the pines.

## **1.4 Background to this research**

In this study, gamma-ray densitometry and image analysis were used to measure wood density, tracheid length and tracheid cross-sectional dimensions. Twelve-millimetre increment core samples were taken from 10.5-year-old trees in field trials at Maxwell in KwaZulu-Natal, South Africa. These trials presented a unique opportunity in that twelve provenances spanning the complete known north to south natural distribution of *P. patula* in Mexico were planted together on a single site. The trees were at an age (10.5 years) where sampling to evaluate wood properties was possible. No fewer than ten open-pollinated, half-sib families represented each provenance. Sufficient families and trees were available to sample a population with an appropriate genetic structure. Many reported wood property studies have been based on too few families. In this study nine trees from nine families from each provenance were sampled. The total size of the population for estimation of genetic parameters in this study was 108 families comprising 972 trees. Twenty-six trees from a local second generation seed orchard seedlot were also sampled in the trials for comparative purposes.

### **1.4.1 Objectives**

The objectives of this study were to answer the following questions about *P. patula* in South Africa.

- i) Are provenance differences important for wood properties? If they are, are we discarding valuable unique material if volume production is our only selection criteria?
- ii) To what extent are the important wood properties under genetic control? Can we select for them?
- iii) Are wood properties correlated with each other? What effect will selection on some properties have on others?
- iv) How strong are age-age correlations within the juvenile core?

To answer these questions, the variation in the wood properties was characterized at the individual tree, family and provenance level at one site in South Africa. Genetic parameters were calculated for all traits and recommendations were made on how best to exploit this variation in an applied breeding program. This thesis reports on the results of the study undertaken to determine the variation and genetic control of wood properties in *P. patula* during 2001 and 2002.

## Chapter 2

### Materials and Methods

#### 2.1 Introduction

This chapter provides information on the origin of the genetic material used in the study and details on which traits were assessed and how the data were analyzed. Subsequent chapters will focus on specific wood properties, the results from their assessment, and the practical implications for tree breeding programs.

All laboratory measurements were conducted at the Council for Scientific and Industrial Research (CSIR), Forests and Forest Products laboratories in Durban, South Africa. Because many of the techniques being used to evaluate wood properties on large numbers of small samples are under development and can provide laboratories with a competitive advantage, this information is considered to be proprietary. Therefore in this chapter, detailed descriptions of laboratory equipment, techniques and methods are not provided. Readers are requested to contact the CSIR directly for more information at their website (<http://ffp.csir.co.za>).

#### 2.2 Genetic material

Since 1986, the CAMCORE Co-operative has sampled 25 provenances and 624 mother trees of *P. patula* in Mexico (Dvorak *et al.*, 2000). A provenance is defined as: " ...*The original geographic area from which seed or other propagules were obtained*", (Zobel and Talbert, 1984). CAMCORE collections represent the most complete coverage of the species natural distribution ever made. The Co-operative has established 93 provenance/progeny trials in Brazil, Chile, Colombia, Mexico, South Africa and Zimbabwe, as well as a number of *ex situ* conservation plantings (Dvorak *et al.* 2000). In December 1990, a series of five CAMCORE trials of open-pollinated *P. patula* family/provenance half-sib seedlots (Table 2.1) were established

by Sappi adjacent to each other, in a single block, at Maxwell in KwaZulu Natal, South Africa. Half-sib seedlots were kept separate by mother tree so the families are represented by maternal half-sibs.

Maxwell can be described as a highly productive *P. patula* site, at an elevation of 1350 m with a mean annual temperature of 16° C. The planting site is located at latitude 30° 03' S and longitude 29° 55' W. The mean annual rainfall is predicted to be 817 mm. This trial series was also established in additional locations by other members of the CAMCORE Co-operative in South Africa and overseas. This study, however, only focuses on a single site.

**Table 2.1** Origin and number of families of the Mexican *P. patula* provenances represented in the CAMCORE trials at Maxwell.

Map Key <sup>1</sup>	Provenance	State or Department	Latitude (N)	Longitude (W)	Elevation Range (m)	Rainfall (mm/yr)	No. of Families
1	Potrero de Monroy	Veracruz	20° 24'	98° 25'	2320 – 2480	1350	17
2	Ingenio del Rosario	Veracruz	19° 31'	97° 06'	2770 – 2870	1346	14
3	Corralitla	Veracruz	18° 38'	97° 06'	2000 – 2230	2500	16
8	Conrado Castillo	Tamaulipas	23° 56'	99° 28'	1500 – 2060	1012	24
10	Tlacotla	Tlaxcala	19° 40'	98° 05'	2750 – 2915	1097	11
11	Pinal de Amoles	Querétaro	21° 07'	99° 41'	2380 – 2550	1350	23
12	Zacualtipán	Hidalgo	20° 39'	98° 40'	1980 – 2200	2047	10
13	Llano de las Carmonas	Puebla	19° 48'	97° 54'	2530 – 2880	1097	20
4	El Manzanal	Oaxaca	16° 06'	96° 33'	2350 – 2660	1348	12
5	El Tlacuache	Oaxaca	16° 44'	97° 09'	2300 – 2620	2000	11
6	Ixtlán	Oaxaca	17° 24'	96° 27'	2600 – 2870	1750	16
7	Santa María Papalo	Oaxaca	17° 49'	96° 48'	2270 – 2720	1100	14
9	Cuajimuloyas	Oaxaca	17° 10'	96° 21'	2450 – 2770	1135	3

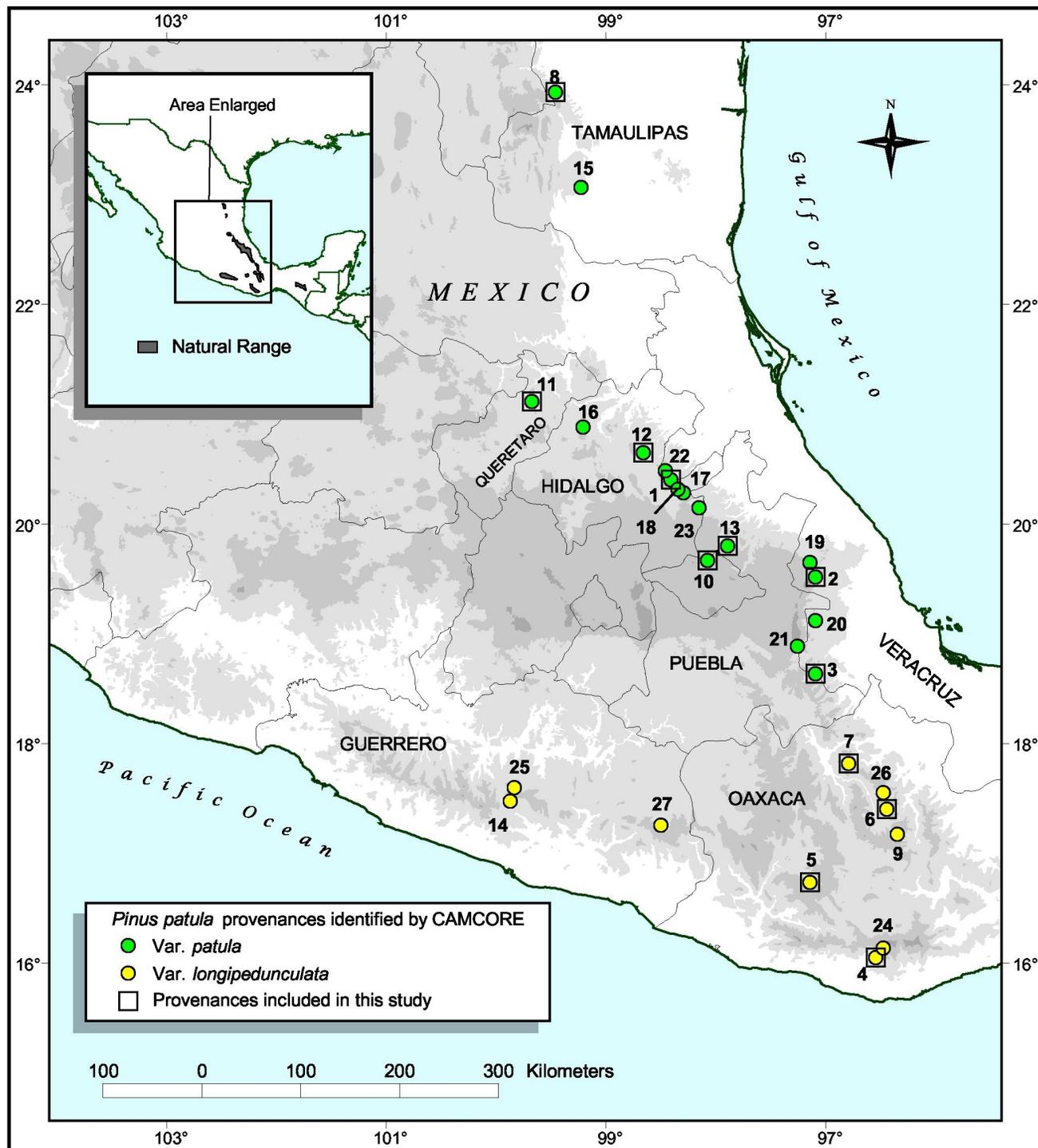
<sup>1</sup> Key to provenance locations in Figure 2.1

The standard CAMCORE design, which is a randomized complete block design with 9 replications and 6-tree row plots, was used for all trials. Trees were established at a 3.0 x 3.0 m spacing. Four local *P. patula* seedlots (M2999, M2997, M3404 and 28222) and *Pinus elliottii* were included as controls. The *P. patula* control lots represent material from breeding programs in South Africa at various levels of improvement. The trials were 10.5 years old when assessed and offered a unique opportunity to sample material from the entire *P. patula* geographic range (Figure 2.1) grown on one site in South Africa, to determine the extent that wood properties are under genetic control at the provenance, family and individual tree level.

Twelve of the thirteen provenances planted at Maxwell were selected for the study (Figure 2.1). The Cuajimoyas provenance was excluded, because it was represented by too few families. The provenances included in this study span the complete known north to south distribution of *P. patula* in its natural range in eastern Mexico, and include provenances representing both var. *patula* and var. *longipedunculata*.

Wood properties often have only a weak or no genetic correlation with growth and stem form traits (Zobel and Jett, 1995). Many papers covering this topic, and summarized by Zobel and van Buijtenen (1989), report little or no relationship between growth rate and wood properties. Although half-sib families and individual trees were selected on the basis of their growth for this study, it is assumed that for purposes of the genetic analysis of the wood properties, that this is a random sample from the population.

The nine best families were selected from each of the twelve provenances on the basis of eight-year growth data. The best tree from each row plot in each of the nine replications in the trial, in which the family was being sampled, was chosen for initial, non-destructive sampling. The genetic structure of the material in this study was therefore made up of 12 provenances with nine families per provenance and nine



**Figure 2.1** Natural distribution of *P. patula* identified by CAMCORE in Mexico. Provenances included in this study are indicated by a square. Map© produced by William Woodbridge, Data Manager, CAMCORE.

trees per family, or 972 trees, excluding controls. This sampling strategy was intended to create a completely balanced data set. Twenty-six trees from the local South African control lot M2999, a second generation, seed orchard, bulk seedlot, were also sampled to provide a baseline representing a local *P. patula* landrace for comparison. The total sample size of the study was 998 trees. A complete list of the families can be found in Appendix 1.

In a project such as this where it is the objective to detect small genetic differences, environmental variation between trees should be reduced to a minimum. It was therefore an advantage to be able to sample material from twelve provenances grown on a single site where the trees included in the study were subject to the same edaphic factors and the same silvicultural conditions. The most likely departure from environmental uniformity is that due to micro-edaphic factors. It is assumed that this variation would be randomly distributed across the experimental site.

### 2.3 Number of trees per family

If prior information is available, an optimum family size to maximize the precision of genetic parameter estimates can be determined using the following procedure. The underlying assumption is that dominance, epistasis and maternal effects are absent .

The intraclass correlation from a one-way ANOVA is:

$$\rho = V_b / (V_b + V_w) \dots\dots\dots [2.1]$$

$$\text{with approximate variance } V(\rho) \approx 2(1-\rho)^2(1+n\rho)^2/nT \dots\dots\dots [2.2]$$

(Robertson, 1959) where;

n = number per family,

N = number of families,

T = total number.

$V(\rho)$  is a minimum when  $n\rho=1$  so  $\rho=1/n$  and the optimum family size  $n \approx 1/\rho$ .

For half-sibs  $\rho \approx 1/4h^2$  so,

$$n=4/h^2 \dots\dots\dots[2.3]$$

Assuming the  $h^2$  is known, the optimum family size can be calculated. Published estimates for  $h^2$  for wood properties show that they are in the range 0.3 to 0.8 (Smith, 1966, Zobel and Jett, 1995). For various  $h^2$  the optimum family size would be:

$$h^2 = 0.3 \quad n = 13$$

$$h^2 = 0.4 \quad n = 10$$

$$h^2 = 0.5 \quad n = 8$$

$$h^2 = 0.6 \quad n = 7$$

$$h^2 = 0.7 \quad n = 6$$

$$h^2 = 0.8 \quad n = 5$$

Based on previously published heritability estimates, these scenarios, and practical limitations, a family size of nine individuals was deemed to be close to the optimum for the accurate determination of genetic parameters for the wood properties being assessed.

## 2.4 Sampling procedure

Field sampling of the trees was conducted during August and September 2001. Where possible, forked and leaning trees were avoided because of the concern that they might have had reaction wood. In some cases where there was no option other than to sample a leaning tree, the sample was taken at  $90^\circ$  to the lean in an attempt to avoid compression wood. Twelve-millimeter increment cores were extracted using a Trecor™ HW300 corer powered by a petrol-motorized Tenaka drill.

Some authors have reported that neither wood density nor tracheid lengths vary significantly with the compass direction from which samples are collected (Ringo and Klem, 1986). To maintain a consistent approach in this study, one bark-to-bark 12 mm increment core was taken from each tree in an east-west orientation at 1.2 m above ground. For some samples, where the pith had been missed during the coring process, some of the inner most rings (two and three) were not present. Although this may cause some bias in the results it is almost impossible to hit the pith with every sample, this limitation has to be accepted when taking large numbers of non-destructive samples.

Cores were air dried at the Shaw Research Centre, Tweedie, South Africa, and then transported to the Council for Scientific and Industrial Research (CSIR), Forests and Forest Products laboratories in Durban, South Africa for measurement of wood properties. Each core was separated into two halves at the pith. Densitometry and tracheid length analyses were carried out on a randomly selected half or radial (pith-to-bark) core. The second half of the core was retained for the determination of cellulose, lignin and polysaccharide yield using near infrared (NIR) techniques. All analyses were performed on un-extracted cores. Prior to analysis in the densitometer, no attempt was made to control the moisture content of the samples. However, samples from each replication were stored together for a number of weeks prior to measurement in order to ensure some uniformity in air dry moisture content within a particular replication.

Samples for the densitometer were prepared using a specially developed electric saw with a tungsten carbide-tooth sawblade. The 12 mm core was clamped into a moving platform with the tracheids orientated vertically, as they would be in a standing tree. Each core was machined to produce a 12 mm deep x 2 mm wide radial section from the centre of the core. The outer portions from the core were retained for tracheid length analysis.

## 2.5 Density measurement

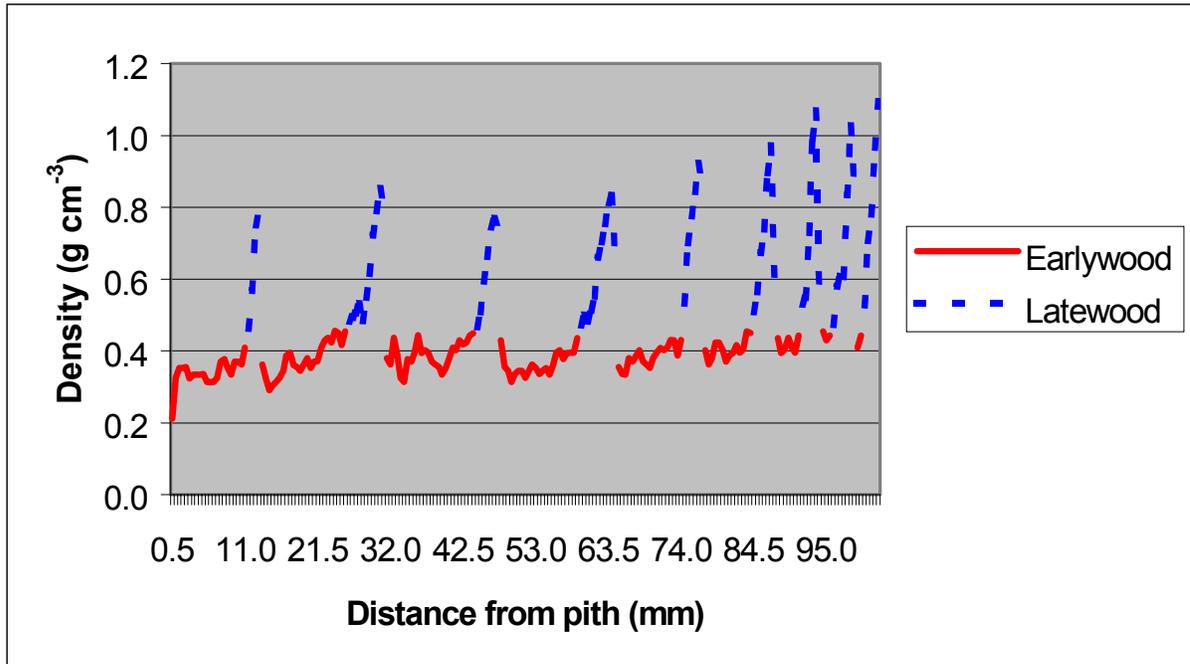
Wood density was determined using 60KeV collimated soft gamma radiation from an Americium<sup>241</sup> energy source. Malan and Marais (1991) showed that the linear attenuation coefficient of wood correlates well with its gravimetric density. Gamma ray densitometry therefore provides a quick and highly reliable method of assessing wood density. In this study, a fully computer controlled data acquisition system and specimen holder with a stepper motor drive, allowing precise 0.5 mm incremental movement of the sample and an individual scanning field of 0.5 mm, was used. For further details on the equipment readers are referred to the paper by Malan and Marais (1991). Samples were processed in replication batches. Wood density was measured every 0.5 mm, so complete pith-to-bark profiles could be drawn for each sample. Weighted mean density (WMD) was calculated for each core using the formula and approach described below (Section 2.11). In this thesis, wood density is expressed in  $\text{g cm}^{-3}$ .

## 2.6 Earlywood - latewood delineation

The ratio of latewood to earlywood is also important because it has a large influence on wood density. The genetic control of the wood density components, which consist of earlywood density, latewood density and latewood percent, have all been reported to be strong (Zobel and Jett, 1995). None of these however, have so far been found to have a higher heritability than overall density and these components have had limited value in improving selection efficiency for overall density. *P. patula* is grown on short pulp wood rotations of 15-20 years in South Africa. With short rotations, the earlywood makes up a large proportion of the juvenile core and it could play a more important role in determining the overall density of the whole tree.

In this study, data were partitioned into earlywood and latewood using a density criterion of  $0.460 \text{ g cm}^{-3}$ . An example is presented in Figure 2.2. Varying criteria have been used to delineate earlywood and latewood. Cown *et al.* (1992) used a

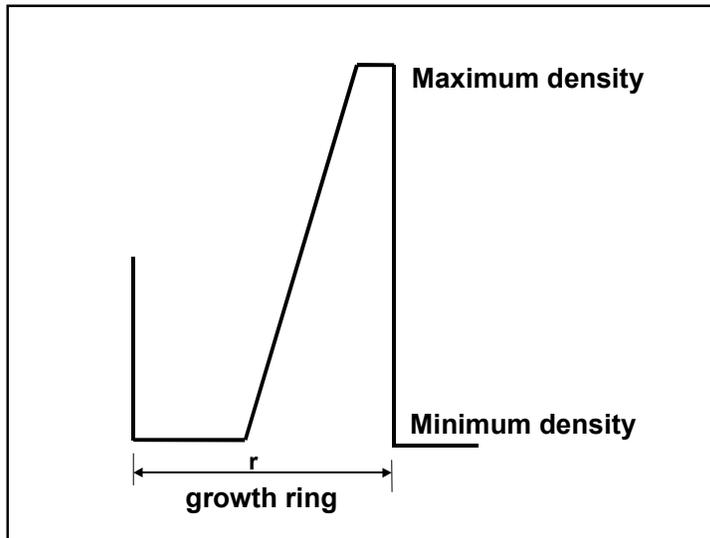
value of  $0.400 \text{ g cm}^{-3}$  and Nyakuengama *et al.* (2000) used a value of  $0.500 \text{ g cm}^{-3}$  for *P. radiata*. Worrall *et al.* (1977) used a value of  $0.600 \text{ g cm}^{-3}$  to delineate latewood in *P. caribaea* grown in Fiji. It appears in most cases the choice of a value to delineate the earlywood and latewood has been an arbitrary one. It was also confirmed by inspecting individual core density profiles that no sample had what was obviously earlywood with density values above the delineation point ( $0.460 \text{ g cm}^{-3}$ ). After partitioning the data, mean latewood density (MLWD) and mean earlywood density (MEWD) were calculated on a per core basis. The percentage of latewood (PLW) was derived on a linear radial basis.



**Figure 2.2** Example of earlywood latewood delineation using  $0.460 \text{ g cm}^{-3}$  as a boundary.

## 2.7 Growth ring width

Growth ring width (in millimeters) was determined for each ring using customized software (CSIR, 2002) and the density profiles from the densitometer. For some rings close to the pith, rings were often not distinct or missing.



**Figure 2.3** Method of determining ring width from a densitometric trace.

Ring width was determined as the distance between the minimum densities that defined the beginning and end of a growth ring (Figure 2.3).

## 2.8 Age trends

Juvenile wood formed near the pith throughout the trunk of a tree can be significantly different from wood produced in the outer rings, termed mature wood. Defining what is juvenile wood can be difficult and is to some degree subjective. There is no clear separation in a tree trunk between juvenile and mature wood, the region where one type of wood starts and the other stops is frequently referred to as transition wood (Zobel and Sprague, 1998). Given the age of the trees in this study, the cores sampled are likely to consist of juvenile wood, or in some cases, juvenile and transition wood.

To further investigate this, each core was partitioned into three regions using the ring-width data. The three regions were the inner three rings (R2-4), consisting of wood from rings two, three and four, the middle three rings (R5-7), consisting of wood from rings five, six and seven, and the outer three rings (R8-10), consisting of rings eight, nine and ten. Using the raw data from the densitometer mean density, mean earlywood and mean latewood density were calculated for each region on an individual core basis. Data generated were then used to determine if there were differences between provenances and families within provenances. Density trends with age, and age-age correlations were also investigated.

## **2.9 Tracheid length measurement**

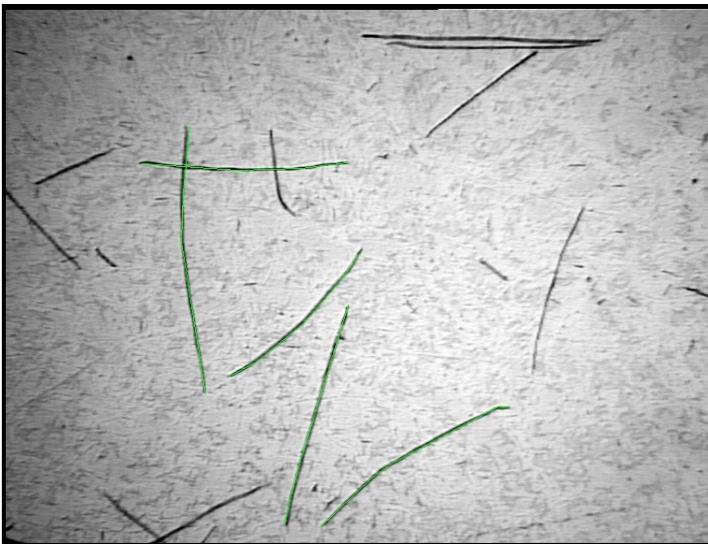
The outer portions from the core after it had been processed for densitometry analysis were used for tracheid length analysis. Since the samples were taken at 1.2 m height on the stem, the first year's ring (from the pith) was not present. Because the trees were 10.5 years of age the last ring was incomplete and therefore not assessed for tracheid length. Growth rings two through ten were therefore available for tracheid length measurement. For some samples, where the pith had been missed during the coring process, some of the inner most rings (two and three) were not present.

Burley *et al.* (1972), found that it was not necessary to separate earlywood and latewood in *P. patula* when determining tracheid length. Sappi (unpublished data) have found similar results for *P. patula*. Therefore, a composite sample of earlywood and latewood was removed from every second ring (rings two, four, six, eight and ten) for maceration. This frequency of assessment was deemed sufficient to provide a suitable pith-to-bark trend, and phenotypic and genetic correlations on a ring-ring and age-age basis. The excised wood was submerged in a 50:50 mixture of glacial acetic acid and hydrogen peroxide (30% vol.) for three days at 60°C. Tracheids were

then teased apart, suspended in distilled water and a sub-sample was mounted on a glass slide.

The length of 50 random whole tracheids were measured on each slide (made up from a ring) using the Videoplan option of a Kotron image analyzer, at the Council for Scientific and Industrial Research (CSIR), Forests and Forest Products laboratories in Durban, South Africa. Whole tracheids are clearly visible and can be identified by their tapering ends (Figure 2.4).

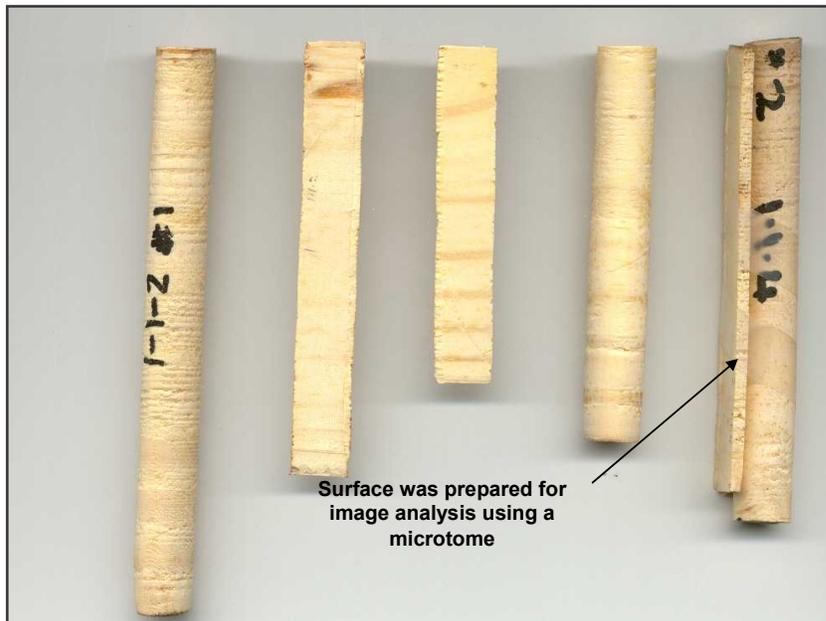
Mean tracheid length was then calculated for rings two, four, six, eight and ten. To estimate within core age-age correlations and genetic parameters, it was assumed that tracheid length for ring two was representative of what could be expected from a core sample taken from a two-year-old tree. Similarly, mean tracheid length from a core for a four-year-old tree was calculated as the mean tracheid length from rings two and four. This procedure was repeated and mean tracheid length was estimated for a two, four, six, eight and ten-year-old tree. No area weighting was applied to the data.



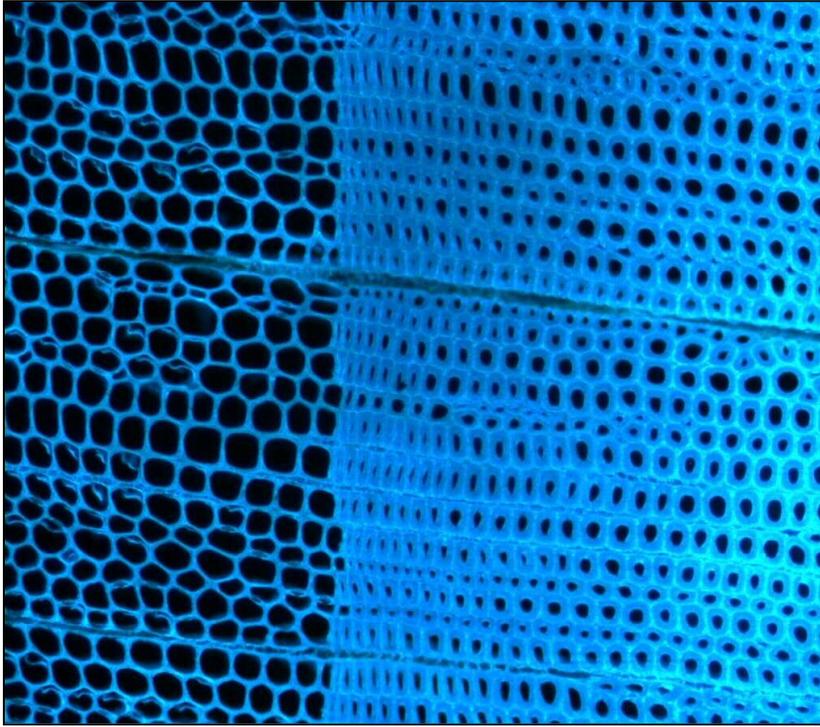
**Figure 2.4** Example of tracheids selected for measurement (highlighted in green).

## 2.10 Tracheid cross-sectional properties

The same section of the core used for the densitometry was used to measure tracheid cross-sectional properties (Figure 2.5). After a freshly-cut surface was exposed using a modified sliding microtome, wood strips were examined in transverse section using a Leica DMLB microscope (Leica, Austria) fitted with fluorescent illumination in the UV range. Images were captured digitally (Figure 2.6), and wood anatomical features quantified using Leica Q-Win image analysis software.



**Figure 2.5** Typical pith-to-bark core and radial sections used when measuring wood density with a densitometer and tracheid cross-sectional properties using an image analysis system.



**Figure 2.6** Example of a digitally captured image using the Leica DMLB microscope, x10 magnification.

The image analysis system first identifies cell lumen and measures its area assuming a circular shape. Lumen diameter (LD) is derived from this measurement. It then identifies boundaries between cells (middle lamella), and calculates cell area within it (including lumen), also assuming roundness. Based on this, cell wall thickness (WT) is derived as:

Cell wall thickness = tracheid diameter - lumen diameter

In addition to fibre diameter, the system identifies and measures cell diameter at perpendicular angles which give tangential (TD) and radial cell diameters (RD).

For each sample, every odd millimeter (mm 1, mm 3, mm 5,.....mm  $n$ , where  $n$  is the last odd millimeter in the radius of the core) along the transverse section from pith-

to-bark was measured at a x10 magnification. At every measurement point the number of individual tracheids measured varied from 300 to 900. Large data files ranging from six to nine megabytes were generated for each sample. Data were written to Excel spreadsheets using a customized macro.

A customized application Image© (Sappi, 2002) was developed to manage the spreadsheet or text based image analysis and density data. The program was designed to maintain the raw data, summarize it, and present it in graphical form for preliminary analysis. The macro used to write the image analysis data to a spreadsheet does not allocate a distance from the pith to the measurements. Image© was designed to do this and to match the density data to the tracheid cross-sectional data. Image© automatically calculates a mean density for the two densitometer measurement points that correspond to the distance (measurement point) where the tracheid cross-sectional properties were measured and writes this to a database , for example:

Density for millimeter one = (Density 0.5 mm + Density 1.0 mm)/2, this corresponds to the tracheid cross-sectional properties from millimeter one.

Four additional tracheid properties were derived using the data from the image analysis system. It was assumed that a tracheid cross-sectional profile was an ellipse. They were mean tracheid area (TArea), mean number of tracheids per square millimeter (NoTrach), mean percentage of cell wall per square millimeter (PCell) and Runkel Ratio (RR), derived as follows:

$$TArea = RD \times TD \times \pi, \text{ where } \pi = 3.141592654 \dots \dots \dots [2.4]$$

$$NoTrach = 1000000/TArea \dots \dots \dots [2.5]$$

$$PCell = ((WArea \times NoTrach)/1000000) \times 100, \text{ where } WArea = \text{wall area} \dots \dots \dots [2.6]$$

$$RR = (2 \times WT)/LD \dots \dots \dots [2.7]$$

To be able to make a comparison with the published reports of Nyakuengama *et al.*, (1999) and Shelbourne *et al.* (1997), tracheid diameter profiles (radial and tangential) and wood density data were used to derive the same variables as produced by SilviScan® analysis of radial wood strips. Evans *et al.* (1995) provide details of assumptions and formulae that are used by SilviScan® software. The additional tracheid cross-sectional parameters were; coarseness (CS), specific surface (SS), perimeter (PM) and wall thickness (WTS).

### 2.11 Parameter area weighting

To calculate the average value for a sample, the following method was used. Area weighted means were calculated for each core and each trait using the formula below.

Let  $p$  = parameter of interest, e.g. Wall thickness.

The value for the parameter  $p$  is the average value for a 1 mm cross-section of the tree (except for density where  $p$  is the average value for a 0.5 mm cross section).

The cross section area of a tree at A is:

$$A = \pi x_2^2 - \pi x_1^2,$$

where  $x_1 = x_2 - 1$ , (for density  $x_2 - 0.5$  would be used).

So therefore  $A = \pi(x_2^2 - (x_2 - 1)^2)$  and solving;

$$A = \pi(2x_2 - 1).$$

So the weighted average value for  $p$  over the sample is :

$$\bar{p} = \frac{\pi \sum_i^n (2x_i - 1)p}{\pi \sum_i^n (2x_i - 1)} = \frac{\sum_i^n (2x_i - 1)p}{\sum_i^n (2x_i - 1)} \dots\dots\dots[2.8]$$

This method assumes that the cross section of the stem is circular. It is not possible to quantify the error associated with the failure of this assumption. Weighted means take into account where the measurement was taken in the radius and therefore have a closer relationship to the value that could be expected from a whole disk taken from a tree. This method was also used in the very comprehensive wood study of *Pinus patula* conducted by Birks and Barnes (1991). To maintain consistency, this method was also applied to the tracheid cross-sectional data.

## 2.12 Statistical models and analysis

The statistical analysis was carried out using Proc GLM in SAS® ver 8.0 (SAS Institute Inc. 1999). The following fixed model was used to calculate provenance least squares means.

$$y_{ijk} = \mu + rep_i + prov_j + (rep*prov)_{ij} + \varepsilon_{ijk} \dots\dots\dots[2.9]$$

where;  $y_{ijk}$  = weighted mean for trait of the  $k^{th}$  tree in the  $i^{th}$  rep and  $j^{th}$  provenance  
 $\mu$  = overall mean  
 $rep$  =  $i^{th}$  rep effect,  $i = 1, \dots, 9$   
 $prov_j$  =  $j^{th}$  provenance effect  $j = 1, \dots, 13$   
 $(rep*prov)_{ij}$  = interaction between the  $i^{th}$  rep and  $j^{th}$  provenance  
 $\varepsilon_{ijkl}$  = random error associated with  $i^{th}$  rep,  $j^{th}$  provenance and  $k^{th}$  tree  
 where  $\varepsilon_{ijk} \sim iid(0, \sigma^2)$

To calculate family within provenance least squares means the model was modified to include a family within provenance term.

$$y_{ijk} = \mu + rep_i + prov_j + (rep*prov)_{ij} + fam(prov)_{jk} + \varepsilon_{ijk} \dots \dots \dots [2.10]$$

where  $\mu$  = overall mean

$rep_i$  =  $i^{th}$  rep,  $i = 1, \dots, 9$

$prov_j$  =  $j^{th}$  provenance effect,  $j = 1, \dots, 12$

$(rep*prov)_{ij}$  = interaction between the  $i^{th}$  rep and  $j^{th}$  provenance

$fam(prov)_{jk}$  =  $k^{th}$  family within  $j^{th}$  provenance effect.

$\varepsilon_{ijk}$  = random error associated with  $i^{th}$  rep,  $j^{th}$  provenance,  $k^{th}$  family within  $j^{th}$  provenance.

To test for normality for all traits, residuals were plotted against fitted values. None showed any detectable trends or patterns. It can therefore be said that the conditions that  $\varepsilon_{ijk} \sim iid(0, \sigma^2)$ , has been met for these data, and the standard ANOVA assumptions, are valid.

### 2.13 Genetic parameter estimation

Prior to the estimation of genetic parameters, control seedlot M2999 was deleted from the data set as it was not part of the population of interest. Using the statistical model [2.10] described in the previous section, variance components and variances of variance components were determined using Proc VARCOMP (method = REML) in SAS®.

Using the variance components, the following parameters were calculated:

Phenotypic variance within-provenance ( $\sigma^2_{phen}$ ) was estimated as:

$$\hat{\sigma}_{\text{phen}}^2 = \hat{\sigma}_{\text{F}}^2 + \hat{\sigma}_{\text{error}}^2 \dots\dots\dots[2.11]$$

where  $\hat{\sigma}_{\text{F}}^2$  = family within provenance variance,  
and  $\hat{\sigma}_{\text{error}}^2$  = error variance or within family variance.

A phenotypic coefficient of variation (CV) was calculated as:

$$\text{CV} = \hat{\sigma}_{\text{phen}} / \bar{y} \dots\dots\dots[2.12]$$

where  $\bar{y}$  = the trait mean. Also a genetic coefficient of variation (GCV) was calculated as:

$$\text{GCV} = \sqrt{3\hat{\sigma}_{\text{F}}^2} / \bar{y} \dots\dots\dots[2.13]$$

When calculating genetic parameters for half-sibs a co-efficient of relationship of 0.33 was used. This was based on the assumption that full-sibs do occur in matings from open-pollination and at least some inbreeding must occur in natural stands (Squillace, 1974). Furthermore, the CAMCORE Co-operative has used a co-efficient of relationship of 0.33 when calculating genetic parameters for growth traits because some of the *P. patula* trees selected in wild populations in Mexico were assumed to be inbred to some degree. To provide comparable parameters from this study, it was decided to accept the assumptions stated above and standardize on a co-efficient of relationship of 0.33. Therefore, additive variance was calculated as:

$$\sigma_{\text{A}}^2 = 3\hat{\sigma}_{\text{F}}^2 \dots\dots\dots[2.14]$$

Single-site (or biased) individual ( $h_{\text{b}}^2$ ) and family heritability estimates within provenance ( $h_{\text{f(b)}}^2$ ) were estimated for all traits using the formula:

$$h_{\text{b}}^2 = 3\hat{\sigma}_{\text{F}}^2 / \hat{\sigma}_{\text{phen}}^2 \dots\dots\dots[2.15]$$

$$h^2_{f(b)} = \hat{\sigma}_F^2 / (\hat{\sigma}_F^2 + \hat{\sigma}_{error}^2/b), \dots\dots\dots[2.16]$$

where b is the number of replications, in this case b=9.

Standard errors were calculated for individual heritability estimates using the following formulae:

$$\text{Var}(h^2_b) = [\hat{\sigma}_A^2 / \hat{\sigma}_{phen}^2]^2 [\text{var}(\hat{\sigma}_A^2) / (\hat{\sigma}_A^2)^2 + \text{var}(\hat{\sigma}_{phen}^2) / (\hat{\sigma}_{phen}^2)^2 - 2\text{cov}(\hat{\sigma}_A^2, \hat{\sigma}_{phen}^2) / \hat{\sigma}_A^2 \cdot \hat{\sigma}_{phen}^2], [2.17]$$

where the standard error =  $\sqrt{\text{var}(h^2_b)}$ .  $\dots\dots\dots[2.18]$   
(Namkoong, 1979)

Provenance variance was expressed on the same scale as heritability, i.e., relative to phenotypic variance within-provenance as:

$$P^2_b = \hat{\sigma}_{prov}^2 / \hat{\sigma}_{phen}^2 \dots\dots\dots[2.19]$$

(Hodge, *et al.* 2001)

Phenotypic (Pearson correlation coefficients) correlations as discussed in the results were calculated using Proc CORR in SAS® at the individual and family level. The same procedure was used to calculate correlations between collection site details and traits of interest.

A phenotypic correlation between two traits can be directly observed. A genetic correlation expresses the extent to which two measurements reflect what is genetically the same character (Falconer, 1981). From a practical aspect, where artificial selection is being practiced, pleiotropic effects, whereby a gene locus or loci influence two traits simultaneously are important. It is important to be able to estimate how the improvement of one trait will cause simultaneous changes in other traits. Additive genetic correlations were calculated using the following formula:

$$r_A = \text{cov}_{XY} / \sqrt{(\sigma^2_{AX} \cdot \sigma^2_{AY})}, \dots\dots\dots [2.20]$$

(Falconer, 1981)

where  $X$  and  $Y$  are the two traits of interest. Additive genetic variance for each trait was calculated as outlined above [2.14].

The covariance between traits  $X$  and  $Y$  was calculated by creating a dummy variable  $(X+Y)$ , and applying the following statistical principle:

$$\sigma^2 (X+Y) = \sigma^2 (X) + \sigma^2 (Y) + 2\text{cov}(X, Y), \text{ therefore} \dots\dots\dots [2.21]$$

$$\text{cov}(XY) = [\sigma^2(X+Y) - \sigma^2 (X) - \sigma^2 (Y)]/2. \dots\dots\dots [2.22]$$

The approximate standard errors of the additive genetic correlations were calculated using the following formula.

$$\text{SE} (r_A) = (1-r_A^2)/\sqrt{2} \sqrt{ \{[\text{SE}(h^2_X) \cdot \text{SE}(h^2_Y)]/h^2_X \cdot h^2_Y \} } \dots\dots\dots [2.23]$$

(Falconer, 1981)

where  $h^2_X$  and  $h^2_Y$  are individual heritability estimates for traits  $X$  and  $Y$ ,  
 $\text{SE}(h^2_X)$  and  $\text{SE}(h^2_Y)$  are the standard error estimates for the respective heritability estimates and,  
 $r_A$  is the additive genetic correlation between traits  $X$  and  $Y$ .

Genetic gains from mass selection were predicted using the following formula.

$$\Delta G = ih^2_X \hat{\sigma}_{\text{phen}X}, \dots\dots\dots [2.24]$$

(Falconer, 1981)

where  $i$  = selection intensity,

$h^2_X$  is the heritability for trait X and,

$\hat{\sigma}_{phenX}$  is the phenotypic standard deviation within-provenance for trait X.

Expected correlated responses from mass selection in trait Y after selecting for trait X were calculated using the following formula.

$$CR_Y = ih_X h_Y r_A \hat{\sigma}_{phenY}, \dots \dots \dots [2.25]$$

(Falconer, 1981)

where  $i$  = selection intensity,

$h_X$  and  $h_Y$  are the square roots of the heritabilities for trait X and Y and,

$\hat{\sigma}_{phenY}$  is the phenotypic standard deviation within-provenance for trait Y.

#### **2.14 Summary of traits measured and derived.**

Traits measured and derived as described above are summarized in Table 2.2. Results from the analyses will be reported on in the following chapters.

**Table 2.2** Summary of traits measured, and derived for analysis.

Trait	Abbrev.	Source
<b>Wood Density Traits</b>		
Weighted mean density	WMD	Densitometer
Mean earlywood density	MEWD	Calculated from densitometer data
Mean latewood density	MLWD	Calculated from densitometer data
Mean latewood percent	PLW	Calculated from densitometer data
Mean density age 2 to 4	R2-4	Calculated from densitometer data
Mean density age 5 to 7	R5-7	Calculated from densitometer data
Mean density age 8 to 10	R8-10	Calculated from densitometer data
Mean earlywood density age 2 to 4	R2-4E	Calculated from densitometer data
Mean earlywood density age 5 to 7	R5-7E	Calculated from densitometer data
Mean earlywood density age 8 to 10	R8-10E	Calculated from densitometer data
Mean latewood density age 2 to 4	R2-4L	Calculated from densitometer data
Mean latewood density age 5 to 7	R5-7L	Calculated from densitometer data
Mean latewood density age 8 to 10	R8-10L	Calculated from densitometer data
Growth ring width (rings 2-10)	GRW2 to 10	Visual - densitometer profiles
<b>Tracheid Length Traits</b>		
Mean tracheid length ring 2	Ring 2	Image analysis - Kotron
Mean tracheid length ring 4	Ring 4	Image analysis - Kotron
Mean tracheid length ring 6	Ring 6	Image analysis - Kotron
Mean tracheid length ring 8	Ring 8	Image analysis - Kotron
Mean tracheid length ring 10	Ring 10	Image analysis - Kotron
Mean tracheid length of an age 2 tree	Age2	Calculated from image analysis data
Mean tracheid length of an age 4 tree	Age4	Calculated from image analysis data
Mean tracheid length of an age 6 tree	Age6	Calculated from image analysis data
Mean tracheid length of an age 8 tree	Age8	Calculated from image analysis data
Mean tracheid length of an age 10 tree	Age10	Calculated from image analysis data
<b>Tracheid Cross-sectional Traits</b>		
Tracheid radial diameter	RD	Image analysis - Leica

**Table 2.2** (continued)

Tracheid tangential diameter	TD	Image analysis - Leica
Tracheid lumen diameter	LD	Image analysis - Leica
Tracheid wall area	WA	Image analysis - Leica
Tracheid wall thickness	WT	Image analysis - Leica
Tracheid Area	TArea	Calculated
No. tracheids per mm <sup>2</sup>	NoTrach	Calculated
Percentage cell wall per mm <sup>2</sup>	PCell	Calculated
Runkel Ratio	RR	Calculated
Coarseness (SilviScan®)	CS	Calculated
Wall Thickness (SilviScan®)	WTS	Calculated
Specific Surface (SilviScan®)	SS	Calculated
Perimeter (SilviScan®)	PM	Calculated

## Chapter 3

### Variation and Genetic Control of Wood Density Traits, Growth Ring Width and Density Age Trends

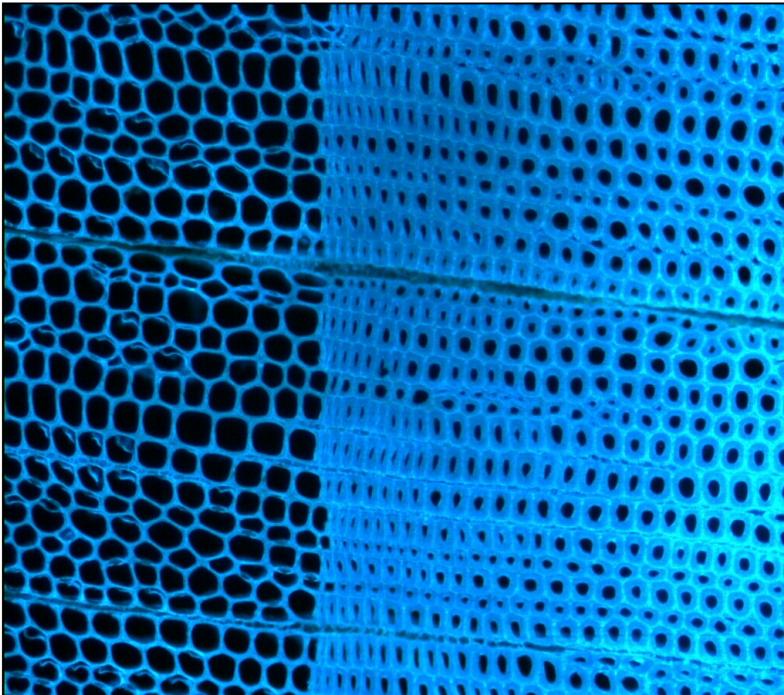
#### 3.1 Review of wood density

Wood density is the term used to express how much wood substance is present in a given volume of wood. It is usually expressed as the ratio of the oven dry weight of wood to its green volume and it is measured in units such as  $\text{kg m}^{-3}$  or  $\text{g cm}^{-3}$ . Wood density is one of the cheapest and easiest wood properties to measure and it can be assessed non-destructively by removing increment cores from a tree. It is a complex characteristic that is interrelated to the proportion of latewood, wall thickness and cell size. Each of these components has an inheritance pattern of its own, but wood density is easier to measure than the individual components.

Most wood density studies in pines have shown that wood density has a direct effect on tracheid yield and paper strength, and on strength and utility of solid wood products (Zobel and Jett, 1995). Van Buijtenen (1967) found that increased wood density and latewood percent results in paper with greater tear strength but in decreased tensile and bursting strengths. Similarly, a large proportion of low density juvenile wood results in low tear and high burst and tensile strength. An important aspect of increased pulp yield associated with the improvement in wood density is that the pulp output of a mill can be increased without changing wood consumption at the mill. Blair *et al.* (1975) have published predictions of gain in pulp yield and tear strength in young loblolly pine through genetic increases in wood density. They found that yield increases from breeding for high wood density could be in the order of 10 to 15% of the mean pulp yield, and tear strength could be increased by about 10% of the mean. Most publications emphasize breeding for high density wood. However, this is only needed for some products, others are best made from low

density wood. It is important to always keep the end product in mind when defining breeding objectives and selection criteria.

One of the biggest sources of variation in wood density in pines is the ratio of earlywood to latewood. The wood characteristics in earlywood and latewood are usually very different. Earlywood has low density and thin tracheid walls (Figure 3.1) and it can easily be recognized as the light brown wider rings in the inner part of a growth ring. Latewood has high density with characteristically thick tracheid walls (Figure 3.1), which make it easy to recognize as the dark brown ring of cells in the outer part of the growth ring. In juvenile wood of pine, the thicker the cell walls the darker the appearance of the latewood band.



**Figure 3.1** Comparison of typical *P. patula* latewood (on the right) with thick tracheid walls and earlywood (on the left) with thin tracheid walls (x 10 magnification). The pith of the tree would be on the right.

The ratio of latewood to earlywood is important because it has a large influence on wood density. The genetic control of the wood density components, which consist of

earlywood density, latewood density and latewood percent, are all strong (Zobel and Jett, 1995). So far none of these have been reported to have a higher heritability than overall density and these components have had limited value in improving selection efficiency for overall density (Zobel and Jett, 1995).

Studies have shown that the inheritance of wood density is strong in pines (Barnes *et al.*, 1994; Birks and Barnes, 1991; Burdon and Low, 1992; Hodge and Purnell, 1993; Loo *et al.*, 1984; and Nyakuengama *et al.*, 1999). Most of the genetic variability is of the additive type, enabling good gains from selection and breeding. Because of its major effect on paper, solid wood products and energy programs, the genetics of wood density has been studied more than any other wood property (Zobel and Jett, 1995). The heritabilities of wood density are generally higher than those for stem form or growth traits, an indication that genetic manipulation of wood density can result in good gains. Published heritabilities for density in pines and hardwoods vary from 0.40 to 0.80 compared to the usual range of 0.15 to 0.25 for many growth traits (Zobel and Jett, 1995 and Shelbourne *et al.*, 1997).

Altering wood density through genetic manipulation is not simple or easy. Density can be changed by growing trees in different environments, but studies on *P. patula* have shown that genotype by environment interaction or rank changes among families, are not significant (Barnes *et al.*, 1994). Unusual wood characteristics are sometimes observed when exotic species are moved into areas that are different to their indigenous environment. It is not correct to assume that a species, or a provenance, will have the same wood properties in the new environment that it had in its native habitat. It is important that new species and provenances are evaluated as early as possible for wood properties, to determine if their wood is commercially acceptable.

Most studies have shown that genetic variation among provenances is negligible, although some studies have shown that there is a slight association between latitude of seed origin and wood density, as well as percent latewood, both of which

increased from northern to southern origins (Zobel and van Buijtenen, 1989). Exploitation of provenance variation in wood density could be crucial for the rapid attainment of a target value for the trait (Burdon *et al.*, 1999), and it is important to determine what variation exists at the provenance level when material is grown in an exotic environment. Very little published information is available on the genetic variation in wood density among individual trees and families for *P. patula*. Of the 58 references provided by Zobel and van Buijtenen (1989) on the genetic control of wood density in pines, only one refers to *P. patula*.

Recently, a comprehensive study examining wood density variation in eight-year-old advanced generation *P. patula* breeding material across six sites in South Africa was completed (Payn, 2001). Payn (2001) found that single-site individual heritability estimates ranged from 0.17 to 0.53. He also reported that family performance was not stable across all sites with type B genetic correlations varying from 0.59 to 0.75 (Payn, 2001). The presence of genotype by environment interaction can complicate breeding strategies, Payn (2001) was able to deal with the genotype by environment interaction by grouping the sites into two classes. Other findings were that both earlywood and latewood density had a strong positive influence on weighted mean core density, the phenotypic correlation of core density with earlywood density was high ( $r = 0.90$ ), while the phenotypic correlation with latewood density was weaker ( $r = 0.67$ ) (Payn, 2001). Birks and Barnes (1991) reported that there were highly significant differences in wood density between families of *P. patula* and that genetic control was almost entirely additive with no variance being attributable to specific combining ability or reciprocal effects. Individual tree heritability estimates for wood density ranged from 0.0 to 0.69. The unweighted average of all heritability estimates for ring five wood density was 0.30 (Birks and Barnes, 1991).

Ladrach (1984) developed a regression model to predict whole tree specific gravity for *P. patula* in Colombia from specific gravity determined at breast height. The age of the trees varied from four to 23 years and the  $R^2$  for the model based on a sample size of 75 trees was 0.93. Ringo and Klem (1980) have also shown that single

increment cores extracted at breast height from 25-year-old *P. patula* grown in Tanzania can be used to estimate whole tree basic density. Their results showed that wood density determined using increment cores underestimate whole tree values by about 4%. Therefore, weighted mean density measured on a core taken at breast height provides a precise ranking and slightly underestimates whole tree density.

In this chapter, the results from examining variation in area weighted mean density, mean earlywood density, mean latewood density and percent latewood at the provenance, family and individual tree level will be discussed. The existence of possible clinal trends will be investigated and the variation in ring width and pith-to-bark trends with age will be discussed. Genetic parameters and correlations among these properties are also presented.

## **3.2 Results and discussion**

### **3.2.1 Weighted mean density**

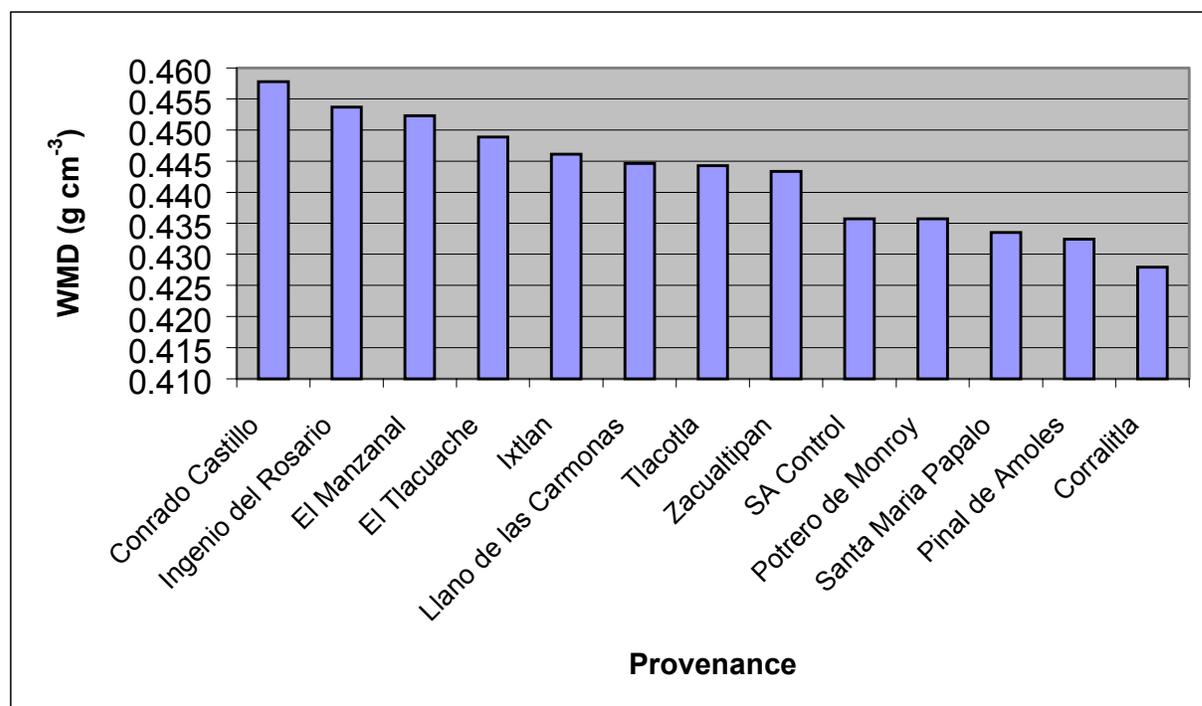
It is almost certain that a tree that exhibits high density wood in the first 4 to 6 years of growth will produce better than average density wood at rotation age (Plumptre, 1978). The trees selected for this study were 10.5-years-old, and wood properties measured now should provide an indication of properties at rotation age, which can vary from 16 to 20 years.

Results from this analysis have shown that differences between provenances for wood density were highly significant ( $P < 0.0001$ ) (Appendix 2). The most northern provenance Conrado Castillo [8]<sup>1</sup>, had the highest area weighted mean density (Figure 3.2). Ingenio del Rosario [2] ranked second and three provenances, El Manzanal [4], El Tlacuache [5], and Ixtlán [6] from the southern extreme of *P. patula*'s distribution were ranked third, fourth and fifth, respectively. These latter

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<sup>1</sup> Number in square brackets refers to provenance number in Figure 3.3

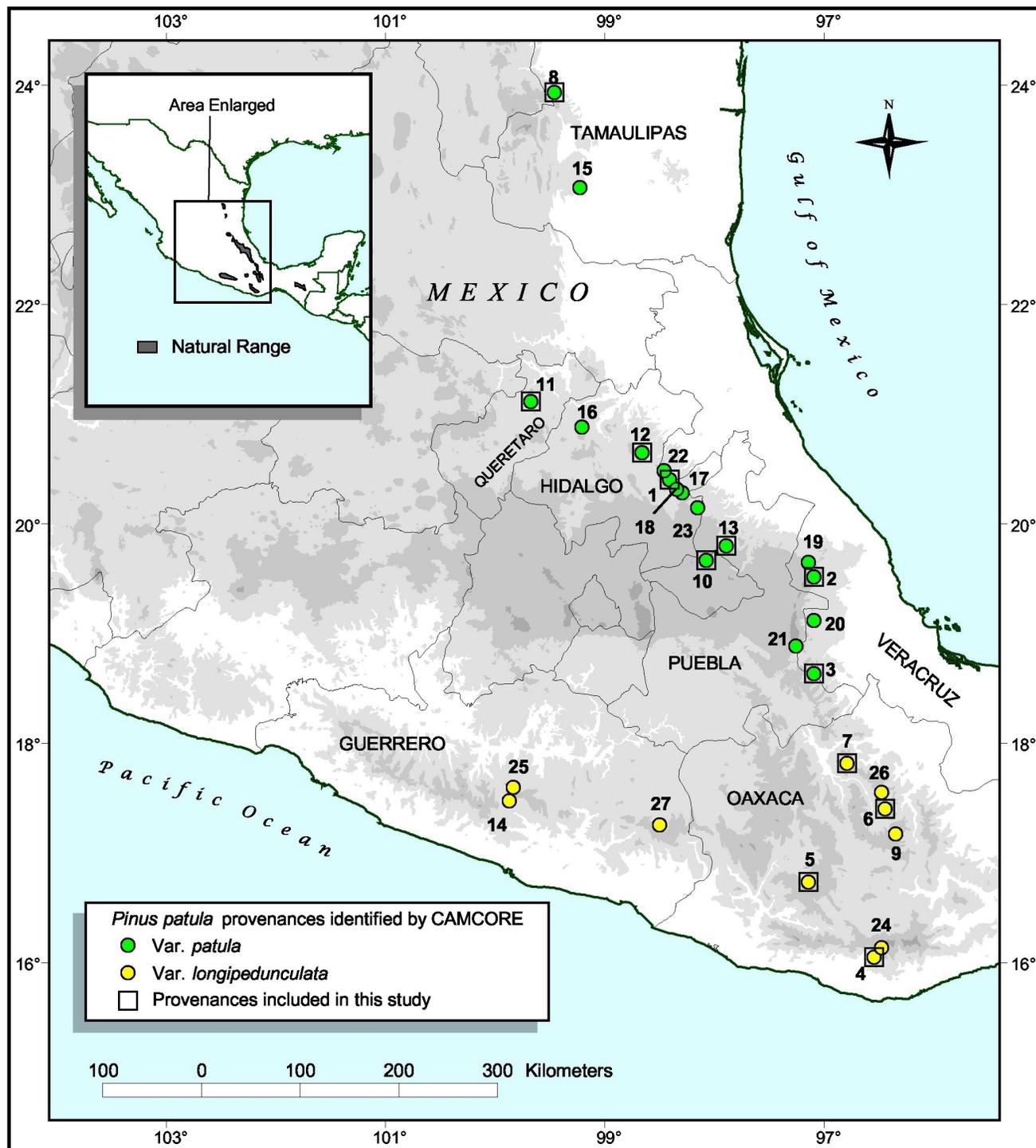
three populations represent *P. patula* var. *longipedunculata* not *P. patula* var. *patula*. Based on these results it appears that *P. patula* populations that occur in the Sierra Madre del Sur in southern Mexico have higher density than those that occur in the Sierra Madre Oriental in eastern Mexico. It also suggests that var. *longipedunculata* may have higher wood density than var. *patula*.



**Figure 3.2** Provenance ranking for area weighted mean density (WMD) at 10.5 years.

Results from the analysis of growth data collected from the same trials, have shown that at eight years of age the local South African seed orchard seedlots and the Potrero de Monroy and Corralitla provenances, were the best for volume production (CAMCORE, unpublished results). Based on these and earlier assessments, 179 selections were made throughout the trials in South Africa. Ninety-three selections were made in families from Potrero de Monroy and Corralitla. Selections from these two provenances therefore account for 52% of all selections made in the trial series. Wood density is an important determinant of total fibre yield. There is cause for

some concern that more than fifty percent of the selections based on volume production made for the next generation of breeding come from two provenances



**Figure 3.3** Natural distribution of *P. patula* identified by CAMCORE in Mexico. Map© produced by William Woodbridge, Data Manager, CAMCORE.

with below average values for wood density. These results demonstrate how important are the routine assessments of wood properties in tree breeding programs. In the absence of this information, a tree breeder could unwittingly be selecting against higher wood density. This aspect will be investigated in more detail at the family level.

Differences between families within provenances were also highly significant ( $p < 0.0001$ ) (Appendix 3). Family 238 from Conrado Castillo had the highest density ( $0.488 \text{ g cm}^{-3}$ ) and family 150 from Ixtlán the lowest density ( $0.409 \text{ g cm}^{-3}$ ) (Table 3.1).

**Table 3.1** Area weighted core mean densities for the top and bottom 10 families.

Top 10 Families		Bottom 10 Families	
Family	Mean ( $\text{g cm}^{-3}$ )	Family	Mean ( $\text{g cm}^{-3}$ )
238	0.488	171	0.421
100	0.486	208	0.421
147	0.480	54	0.419
86	0.477	67	0.418
305	0.474	211	0.416
227	0.471	218	0.416
228	0.467	290	0.414
78	0.466	69	0.409
7	0.466	172	0.409
270	0.465	150	0.409
Trial Mean	0.443		
SD	0.041		

The range in family mean density in this study was  $0.079 \text{ g cm}^{-3}$  or 19% of the population mean. This indicates slightly lower levels of variation at the family level than for growth traits. At age eight the range in family mean diameter varied from 20% to 37% of the population mean for this trial series. This may have implications

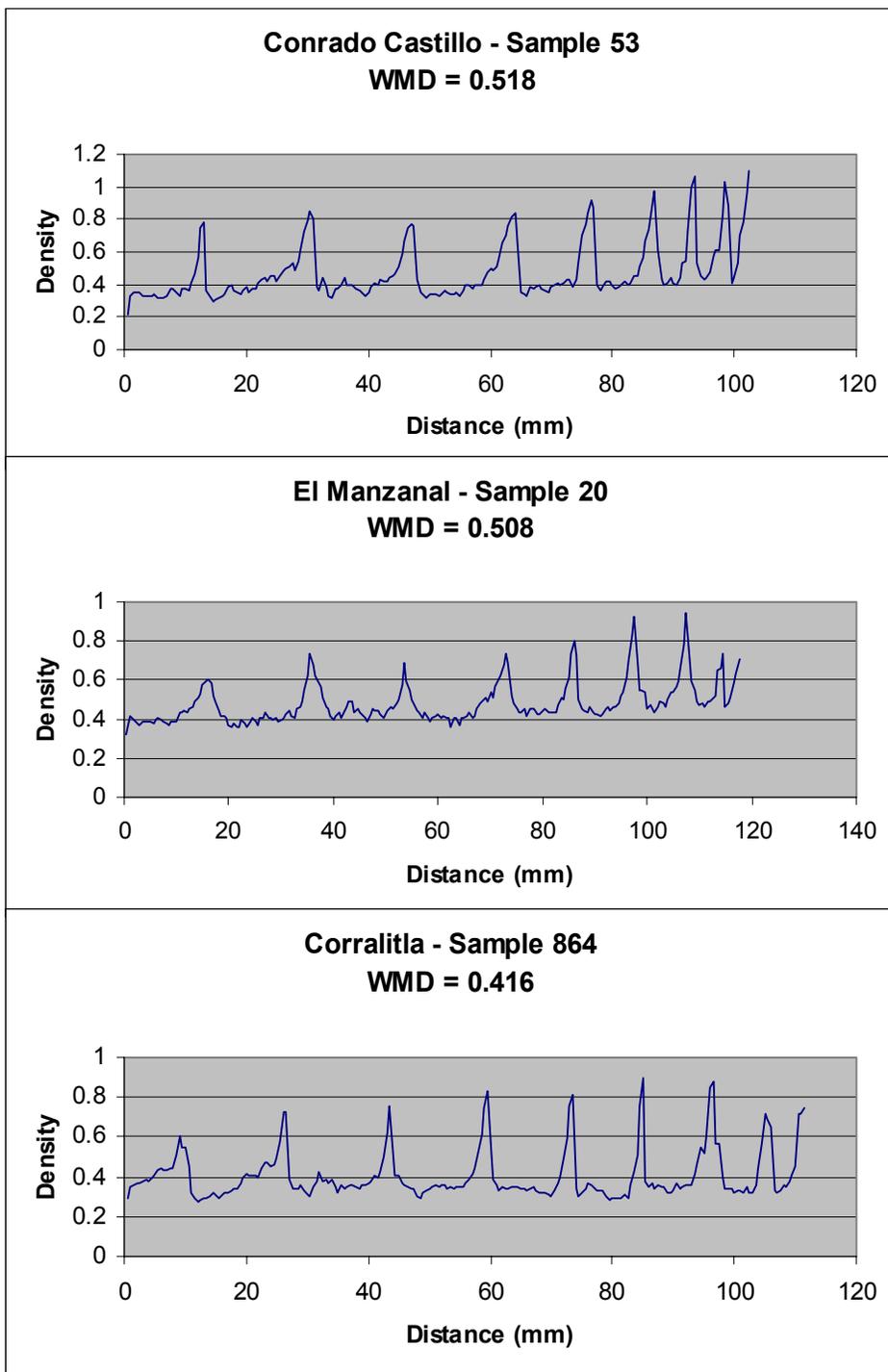
for selection strategy. Similar ranges in family mean density were reported by Payn (2001).

There was a much larger range in density between individual trees. The top ranked and bottom ranked trees in the study had weighted mean densities of  $0.614 \text{ g cm}^{-3}$  and  $0.331 \text{ g cm}^{-3}$  respectively. The range was  $0.283 \text{ g cm}^{-3}$  or 85% of the population mean. The implication of these lower levels of phenotypic variation for breeding will be quantified in Chapter 7.

### 3.2.2 Earlywood and latewood

The wood characteristics in earlywood and latewood are usually very different. Most authors emphasize the importance of variation in latewood percentage as the source of variation in wood density in pines (Zobel and van Buijtenen, 1989). *P. patula* grown for pulpwood in South Africa is grown on short rotations of 15-20 years. The percentage of latewood is likely to have less influence on the overall tree density on short rotation pulpwood crops. Latewood percentage has been shown to increase dramatically from age 22 in *P. patula* grown in Zimbabwe (Burley *et al.* 1970, 1972). This is towards the upper limit of pulpwood rotations in South Africa and suggests that latewood percentage may not be as important for *P. patula* as has been reported for other species.

Pith-to-bark density profiles were graphed for all samples. Differences between density profiles from different provenances were clearly visible. For example in Figure 3.4, sample 864 has noticeably lower density earlywood bands, all have a density close to  $0.350 \text{ g cm}^{-3}$ . On the other hand, the earlywood bands in samples 53 and 20 all have densities close to or greater than  $0.400 \text{ g cm}^{-3}$ . Preliminary indications based on visual inspection of the profiles seemed to indicate that one reason for the provenance variation in wood density might be the proportion of earlywood to latewood and its mean density. This was then investigated in more detail.



**Figure 3.4** Typical pith-to-bark density profiles of a random sample from three provenances representing extremes of the density range in this study.

As outlined in the material and methods a density value of  $0.460 \text{ g cm}^{-3}$  was used to delineate between earlywood and latewood. Compared to European species there is a much smaller difference between the densities of earlywood and latewood in *P. patula* (Fry and Chalk, 1956). Fry and Chalk (1956) carried out a detailed study on twenty three 13-year-old *P. patula* trees grown in Kenya. It was concluded that the mean density of the earlywood in *P. patula* is about half that of the latewood or more (Fry and Chalk, 1956). In this study the mean earlywood density was  $0.365 \text{ g cm}^{-3}$  and the mean latewood density  $0.611 \text{ g cm}^{-3}$ , this equates to a ratio of 0.59. The delineation value used in this study appears to be in line with what Fry and Chalk (1956) reported. For the six sites in his study Payn (2001) reported that earlywood density ranged from  $0.327$  to  $0.346 \text{ g cm}^{-3}$  and latewood density ranged from  $0.611$  to  $0.680 \text{ g cm}^{-3}$ . These estimates are similar to those obtained in this study.

Mean earlywood densities (MEWD), mean latewood densities (MLWD) and mean percentage latewood (PLW) were calculated for each provenance, family and individual tree. These are collectively referred to as density traits in the text. Provenance results and rankings are presented in Table 3.2.

Provenance differences were highly significant ( $p < 0.0001$ ) for both latewood and earlywood traits (Appendix 2). With the exception of the most northern provenance Conrado Castillo, the southern most provenances, El Tlacuache, El Manzanal, Ixtlan and Santa Maria Papalo, all classified as *var. longipedunculata*, had the highest mean earlywood density (Table 3.2). These four provenances also had the lowest mean latewood density (Table 3.2). Wood from these provenances will be more uniform as the difference between latewood and earlywood density is smaller, other tracheid attributes are also likely to differ less. Malan and Hoon (1991) reported that three *P. tecunumanii* provenances had more uniform wood and higher density than *P. patula*. The trees were sampled in trials in South Africa. *P. tecunumanii*, a species that occurs naturally in southern Mexico and Central America, appears to have similar attributes (higher density and more uniform wood) to the most southern

populations of *P. patula*. A clinal pattern may exist for wood properties, this will be investigated in the next section.

**Table 3.2** Provenance mean earlywood density (MEWD), latewood density (MLWD) and percentage latewood (PLW) ranked on provenance mean weighted density. Weighted mean density (WMD) included for comparative purposes.

Provenance	WMD (g cm <sup>-3</sup> )	MEWD (g cm <sup>-3</sup> )	R <sup>1</sup>	MLWD (g cm <sup>-3</sup> )	R <sup>1</sup>	PLW (%)	R <sup>1</sup>
Conrado Castillo	0.458	0.371	4	0.621	8	28.68	3
Ingenio del Rosa	0.454	0.363	6	0.632	4	26.22	5
El Manzanal	0.452	0.390	2	0.557	12	29.99	2
El Tlacuache	0.450	0.392	1	0.553	13	30.17	1
Ixtlan	0.446	0.376	3	0.595	10	27.12	4
Llano de las Car	0.445	0.357	8	0.628	5	24.93	7
Tlacotla	0.444	0.353	13	0.644	1	23.95	8
Zacualltipan	0.443	0.357	10	0.634	2	24.98	6
Potrero de Monroy	0.435	0.354	12	0.633	3	22.29	13
SA control	0.435	0.359	7	0.623	6	23.18	11
Santa Maria Papalo	0.434	0.369	5	0.594	11	23.91	9
Pinal de Amoles	0.432	0.354	11	0.622	7	23.38	10
Corralitla	0.428	0.357	9	0.618	9	22.37	12
Mean	0.443	0.365		0.611		25.65	
SD	0.017	0.016		0.031		4.66	
Minimum	0.428	0.353		0.553		22.29	
Maximum	0.458	0.382		0.644		30.17	
Range	0.030	0.029		0.091		7.88	

<sup>1</sup> Provenance ranking for respective trait.

Corralitla ranked poorly for all three derived density traits, this accounts for its overall low weighted mean density. Potrero de Monroy has the lowest percentage latewood, one of the highest mean latewood densities, and the second lowest mean earlywood density an indication of narrow high density latewood bands. Large differences between latewood and earlywood may not be desirable from a processing perspective. The South Africa control was ranked in the middle for both mean earlywood and latewood density, but had a lower percentage of latewood.

The top twenty families for weighted mean density are presented in Table 3.3.

**Table 3.3** Family mean earlywood density (MEWD), latewood density (MLWD) and percentage latewood (PLW) ranked on family mean weighted density (WMD) for the top 20 families.

Family	WMD (g cm <sup>-3</sup> )	MEWD (g cm <sup>-3</sup> )	R <sup>1</sup>	MLWD (g cm <sup>-3</sup> )	R <sup>1</sup>	PLW (%)	R <sup>1</sup>
238	0.488	0.385	16	0.622	51	35.79	4
100	0.486	0.396	7	0.564	93	43.43	1
147	0.477	0.392	10	0.591	87	37.17	2
86	0.477	0.404	2	0.563	94	34.53	7
305	0.474	0.366	48	0.661	2	27.99	26
227	0.472	0.373	32	0.631	33	30.72	15
228	0.467	0.368	43	0.634	27	29.74	19
78	0.466	0.397	5	0.552	100	35.26	5
7	0.466	0.366	49	0.641	10	28.37	23
131	0.465	0.394	9	0.544	105	34.00	9
270	0.465	0.370	36	0.621	54	27.53	29
44	0.465	0.366	47	0.637	17	27.25	31
261	0.464	0.369	40	0.645	6	28.94	22
125	0.464	0.399	4	0.547	104	34.53	6
286	0.464	0.367	44	0.625	46	30.28	17
225	0.463	0.382	19	0.607	73	33.28	10
262	0.462	0.370	34	0.636	21	28.04	25
154	0.461	0.386	15	0.594	84	29.88	18
51	0.461	0.372	33	0.630	37	28.09	24
53	0.461	0.373	29	0.623	48	29.51	20
Mean	0.443	0.366		0.611		25.65	
SD	0.017	0.016		0.031		4.66	
Minimum	0.409	0.338		0.538		17.80	
Maximum	0.488	0.405		0.662		43.43	
Range	0.079	0.068		0.124		25.64	

<sup>1</sup> Family ranking out of 108 families for respective trait.

At the family level it appears that the main influence on wood density is percentage latewood. Thirteen families are ranked in the top 20 for both weighted mean density

and percentage latewood (Table 3.3). The range between the best and worst family is of a similar magnitude for both weighted mean density and mean latewood density.

However, the ranges for mean latewood density and percentage latewood are much larger. The availability of phenotypic variation at the family level for these two traits may have implications for selection and genetic gain. More gain may be possible by selecting for these traits. At the individual tree level, mean earlywood density ranged from 0.276 to 0.442 g cm<sup>-3</sup>, mean latewood density from 0.497 to 0.711 g cm<sup>-3</sup> and percentage latewood from 6 to 85.7%. High levels of phenotypic variation exist for all traits at the individual tree level.

### 3.2.3 Correlation with collection sites

In the preceding section the possible existence of a clinal pattern for density traits was introduced. A cline is defined as "*a gradient in a measurable characteristic which follows an environmental gradient*" (Zobel and Talbert, 1984). To quantify this, provenance mean density traits (WMD, MEWD, MLWD and PLW) were correlated with collection site climatic data obtained from CAMCORE (CAMCORE, 2002). Climatic data from the collection sites included, latitude (Lat.), longitude (Long.), mean annual precipitation (MAP), mean annual temperature (MAT), elevation and mean monthly precipitation.

Zobel and Jett (1995) state that "*provenances originating in milder climates, which should have adapted to more growing days, should have a later completion of height growth, resulting in lower wood density*". Correlation coefficients for density traits and the four most important collection site parameters are presented in Table 3.4. For these data there were no positive correlations with rainfall (annual or monthly mean) or temperature (Table 3.4). Field trials have shown that the southern provenances of *P. patula* are more susceptible to cold damage, these provenances

originate from milder climates. At the age of assessment these provenances had higher overall density, and therefore, the statement by Zobel and Jett (1995) cannot be generalized to all situations.

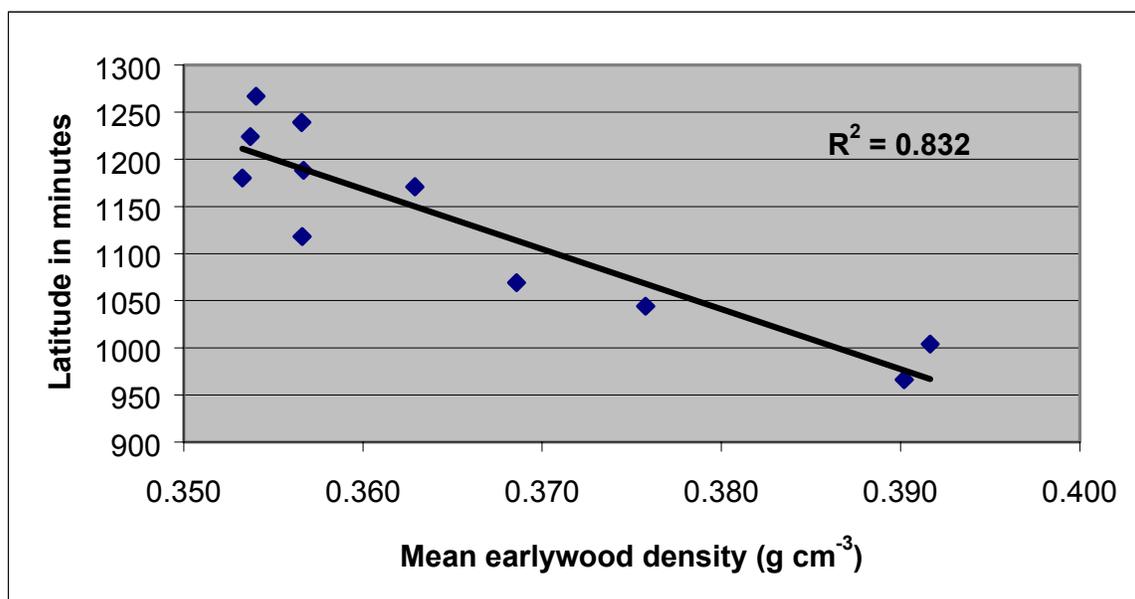
**Table 3.4** Correlation of provenance weighted mean density (WMD), mean earlywood density (MEWD), mean latewood density (MLWD) and percentage latewood (PLW) with collection site latitude, longitude, mean annual precipitation (MAP) and mean annual temperature (MAT). Significant correlations in bold, p-values in brackets.

<b>All twelve provenances</b>				
<b>Variable</b>	<b>Lat. (N)</b>	<b>Long. (W)</b>	<b>MAP (mm)</b>	<b>MAT (°C)</b>
WMD	0.06 (0.853)	-0.06 (0.862)	-0.35 (0.266)	-0.43 (0.167)
MEWD	<b>-0.60</b> (0.040)	-0.53 (0.074)	0.04 (0.897)	0.23 (0.478)
MLWD	<b>0.73</b> (0.007)	0.58 (0.049)	-0.14 (0.674)	-0.45 (0.146)
PLW	-0.29 (0.355)	-0.27 (0.402)	-0.13 (0.698)	0.02 (0.954)
<b>Conrado Castillo excluded</b>				
<b>Variable</b>	<b>Lat. (N)</b>	<b>Long. (W)</b>	<b>MAP (mm)</b>	<b>MAT (°C)</b>
WMD	-0.40 (0.223)	-0.39 (0.240)	-0.27 (0.421)	-0.45 (0.165)
MEWD	<b>-0.90</b> (0.000)	<b>-0.68</b> (0.022)	0.07 (0.833)	0.24 (0.483)
MLWD	<b>0.88</b> (0.000)	<b>0.61</b> (0.048)	-0.11 (0.740)	-0.44 (0.174)
PLW	<b>-0.74</b> (0.010)	-0.53 (0.094)	-0.04 (0.896)	0.05 (0.894)

Mean earlywood density was significantly, but negatively correlated with latitude ( $r = -0.60$ ). The correlation between mean latewood density and latitude was significant but positive ( $r = 0.73$ ). Mean latewood density appears to increase with increasing latitude while mean earlywood density decreases with increasing latitude. The more northerly provenances could be expected to have lower density earlywood and

higher density latewood. Although the correlation between percentage latewood and latitude is not significant, it is negative ( $r = -0.29$ ). The effect of the higher density latewood could be negated by the decrease in percentage latewood in the northern provenances. Conrado Castillo appears to be an outlier provenance as it had the highest weighted mean density (see previous discussion), but is the most northern provenance. It was identified as a possible outlier and deleted from the data. The significant correlations increased in magnitude and significance when this provenance was excluded (Table 3.4).

With Conrado Castillo excluded, the correlation between mean earlywood density and latitude improved dramatically ( $r = -0.90$ ), as did the correlation between mean latewood density and latitude ( $r = 0.88$ ). Three other correlations were also significant (Table 3.4). The data indicate that a distinct clinal pattern exists for wood density in *P. patula* (Figure 3.5). This seems to extend to the results of the study on *P. tecunumanii* (Malan and Hoon, 1991).



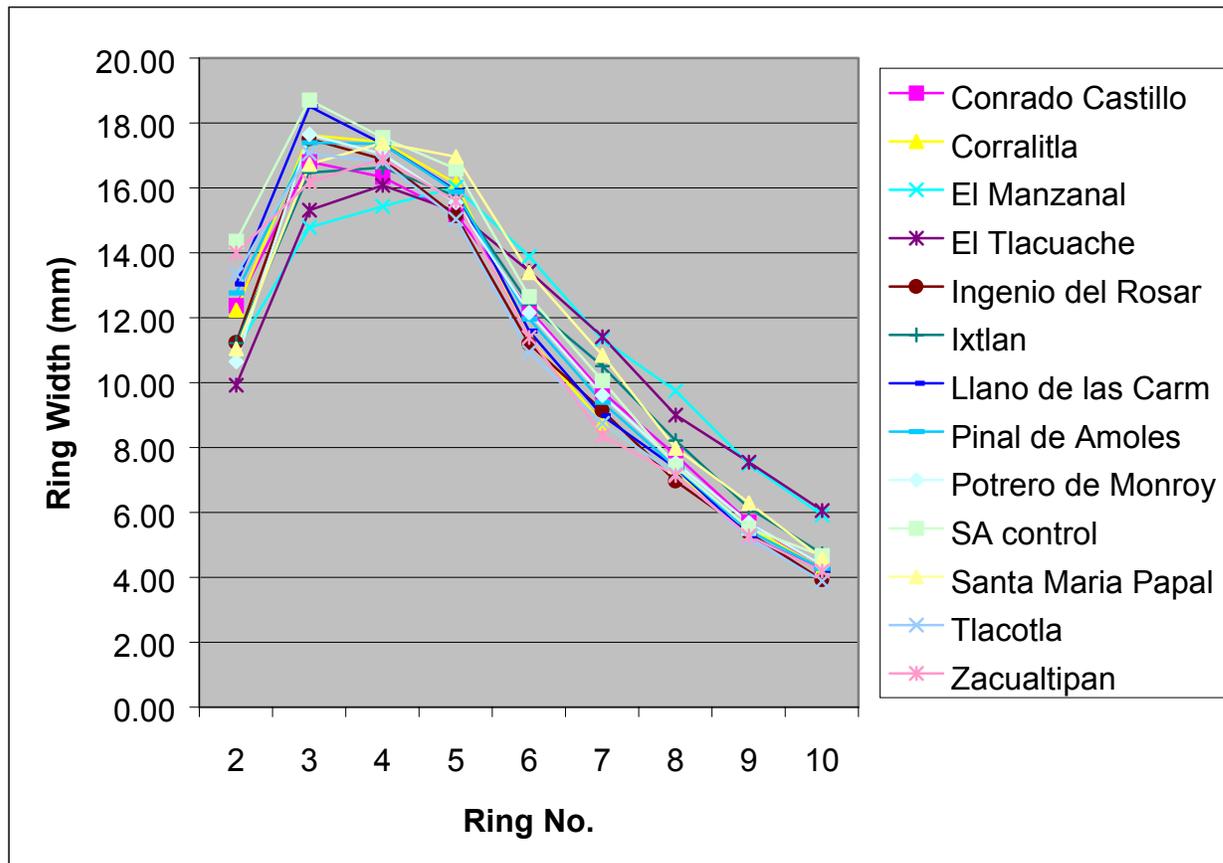
**Figure 3.5** Mean earlywood density plotted against provenance latitude, Conrado Castillo excluded, demonstrating a clear north to south increase (clinal trend) in mean earlywood density.

These findings suggest additional areas of research. Will wood density increase from north to south in natural habitats in Mexico and Central America as the climate changes from temperate to subtropical? Will the difference between earlywood and latewood become less distinct when seeds from these habitats are grown in exotic environments, providing a more desirable raw material? These questions are beyond the scope of this study, but the existence of a possible clinal trend for tracheid length and cross-sectional properties will be investigated and discussed in Chapters 4 and 5.

### 3.2.4 Growth ring width

Barnes *et al.* (1994) reported on the genetic control of ring width, for rings one to six which corresponded to growing years two to seven, for *P. patula* grown in Zimbabwe. Barnes *et al.* (1994) found that treatment differences for ring width were most pronounced between the second and fourth rings. It was speculated that this was because residual nursery and establishment effects had ceased to influence growth and stand competition had not yet set in (Barnes *et al.*, 1994). In this study provenance differences were significant for all growth rings, but family within provenance differences were only significant for growth rings five, six and ten (Appendix 3).

The overall trends in this study were in good agreement with what Barnes *et al.* (1994) reported. Initially ring width increased to age three, reaching a maximum between 14.8 and 18.7 mm (Figure 3.6). After age five ring width decreased rapidly (Figure 3.6). In the Zimbabwean study, ring widths also peaked at age three, but the decline in ring width was more rapid, reaching a growth ring width of approximately 5.0 mm at age seven (Barnes *et al.* , 1994). At Maxwell the grow ring widths reached these same levels at age 10, undoubtedly site has an effect (Barnes *et al.* 1994).



**Figure 3.6** Provenance variation in ring width at 1.2 m with ring number .

For all ages, ring width differences between provenances were highly significant (Appendix 3). From rings six to ten the El Manzanal and El Tlacuache provenances had the widest rings (Figure 3.6). These two provenances also had the highest percent latewood and earlywood mean densities (Table 3.2). There appears to be very little difference between the other provenances after age six (Figure 3.6). Wide growth rings, higher than average earlywood density and a higher percentage of lower than average density latewood seem to account for the overall higher weighted mean density for these two provenances. These characteristics indicate that El Manzanal and El Tlacuache are more likely to have more uniform wood, which would be favored by processors.

### 3.2.5 Pith-to-bark age trends

Juvenile wood, which is formed near the pith throughout the trunk of a tree, can be significantly different from wood produced in the outer rings (mature wood). The juvenile core is particularly prominent in fast grown pines and may comprise the bulk of the volume of thinnings or even the final crop logs harvested on short rotations (Cown *et al.*, 1992). Typical pulpwood rotations in South Africa vary from 16-20 years for *P. patula*.

The determination of the juvenile zone depends upon which wood characteristic is used to define it. Juvenile wood is most commonly based upon wood density (Zobel and Sprague, 1998). The relationship between wood properties and wood age (normally described as distance from the pith) in loblolly pine has been described as a trend characterized by rapidly increasing specific gravity and tracheid length with age, leveling off at seven to 15 rings from the pith (Loo *et al.* 1985). Few reports on where the transition occurs in *P. patula* are available. On the Viphya Plateau, Malawi, the juvenile core of *P. patula* has been reported to persist until 6 to 8 years (Adlard *et al.*, 1979). In South Africa, de Villiers (1966) reported that the juvenile core consisted of the first twelve rings from the pith. Because there is no clear separation in a tree trunk between juvenile and mature wood, the region where one type of wood begins to change into the other is frequently referred to as transition wood (Zobel and Sprague, 1998). Given the age of the trees in this study, the cores sampled are likely to consist of juvenile, and in some trees, a mixture of juvenile and transition wood.

As described in the materials and methods, each core was partitioned into three regions, the inner three rings (R2-4), middle three rings (R5-7) and outer three rings (R8-10). Differences between provenances and families within provenance were highly significant ( $P > 0.001$ ) for all three traits (Appendix 4). El Manzanal and El Tlacuache had high mean densities relative to the other provenances during the first seven years of growth but have dropped off during the last three years (Table 3.5).

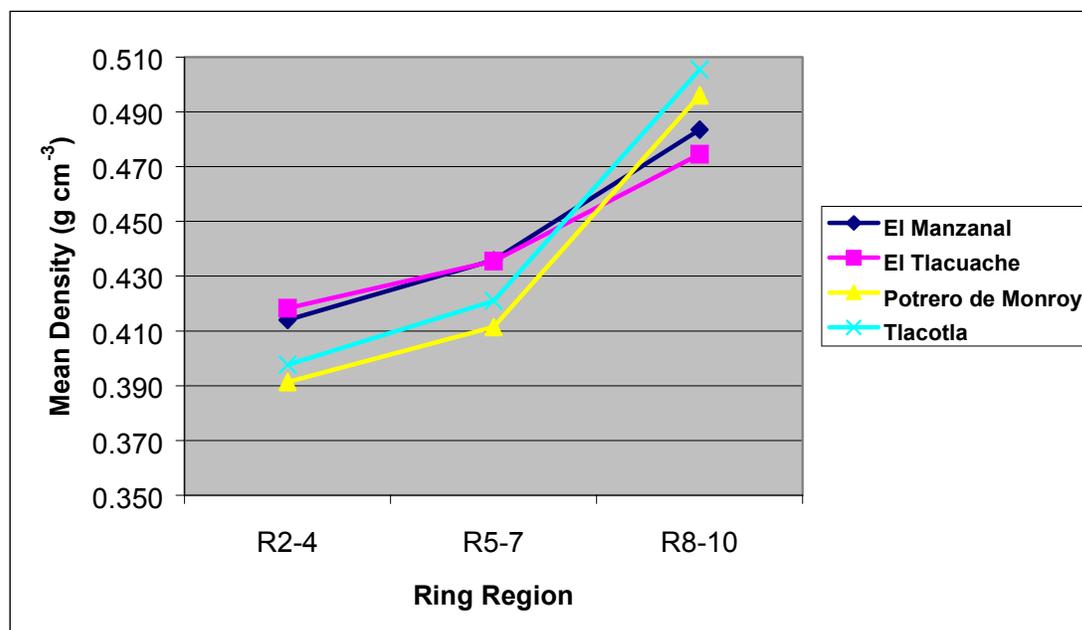
**Table 3.5** Provenance mean densities for core regions representing growth from the 1992-1994 (R2-4), 1995-1997 (R5-7), and 1998-2000 (R8-10) growing seasons.

Provenance	R2-4	R <sup>1</sup>	R5-7	R <sup>1</sup>	R8-10	R <sup>1</sup>
Ingenio del Rosa	0.405	7	0.430	4	0.509	1
Tlacotla	0.398	12	0.421	6	0.505	2
Conrado Castillo	0.420	1	0.435	3	0.504	3
Zacualtipan	0.406	6	0.415	9	0.502	4
Llano de las Carmonas	0.399	9	0.421	7	0.500	5
Potrero de Monroy	0.391	13	0.411	11	0.496	6
Pinal de Amoles	0.398	11	0.408	12	0.491	7
Ixtlan	0.418	3	0.426	5	0.486	8
SA control	0.404	8	0.412	10	0.484	9
El Manzanal	0.414	4	0.436	1	0.483	10
Corralitla	0.398	10	0.404	13	0.477	11
El Tlacuache	0.418	2	0.436	2	0.475	12
Santa Maria Papalo	0.408	5	0.415	8	0.468	13
Mean	0.406		0.421		0.490	
SD	0.0379		0.0399		0.0561	
Minimum	0.391		0.404		0.468	
Maximum	0.420		0.436		0.509	
Range	0.029		0.032		0.041	

<sup>1</sup> Provenance ranking for respective trait.

In contrast the Tlacotla provenances increase in density with age has been dramatic. (Table 3.5). Conrado Castillo constantly ranked among the top three provenances for all core regions and appears to be stable over time. (Table 3.5). The rapid increase could be an indication that the families from Tlacotla have begun producing more mature wood. Tlacotla had the lowest density earlywood and highest density latewood (Table 3.2). Potrero de Monroy and Pinal de Amoles have also responded in a similar manner. Both these provenances had low overall weighted mean densities. At a young age the juvenile core makes up a large portion of the total cross section of the trunk so if the trees were assessed at an older age the overall weighted mean densities of these two provenances may have improved.

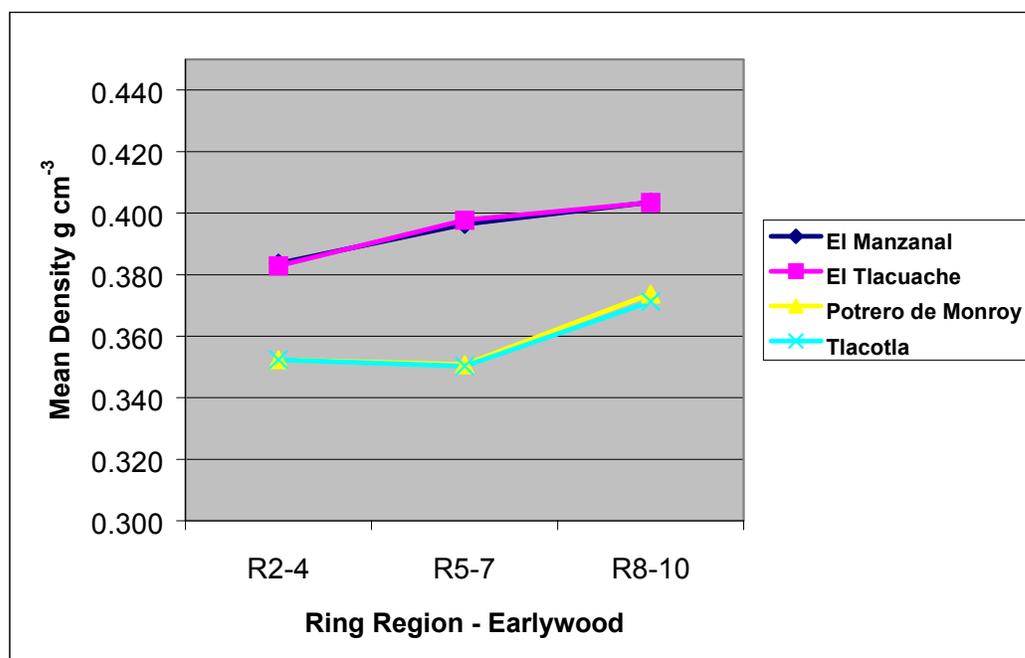
The importance of wood uniformity has been discussed. It may be more important than overall wood density, in earlier discussion it was suggested that El Manzanal and El Tlacuache might have more uniform wood than Potrero de Monroy and Tlacotla. This was investigated further using the density data derived for the three core regions for these four provenances (Figure 3.7).



**Figure 3.7** Mean density by ring region for four selected provenances.

The rate of increase between ring regions R2-4 and R5-7 is relatively uniform and constant for the four provenances, the lines are for practical purposes parallel to each other (Figure 3.7). El Manzanal and El Tlacuache maintain an overall higher mean density. The rate of increase between ring regions R5-7 and R8-10 differs dramatically. The response of Potrero de Monroy and Tlacotla in magnitude and slope of the lines are similar. Their response is however, very different to the response of El Manzanal and El Tlacuache whose increase in density is not as dramatic, indicating that at the age of assessment the pith-to-bark density profile is more uniform.

The rate of increase between ring regions R5-7 and R8-10 was investigated in more detail for the same four provenances by separating the regions into their earlywood and latewood components (Figure 3.8 and Figure 3.9).

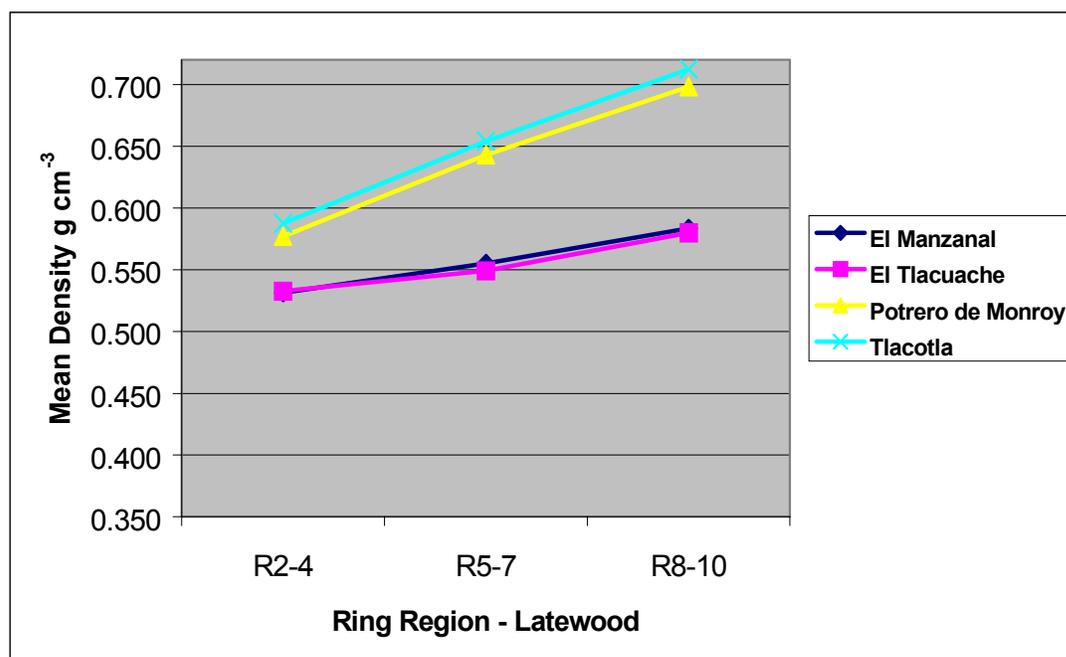


**Figure 3.8** Mean earlywood density by ring region for four selected provenances.

Potrero de Monroy and Tlacotla show a more rapid increase in mean earlywood density after age seven (Figure 3.8) than the southern provenances El Manzanal and El Tlacuache, the rate of increase in earlywood density appears to be slowing for the latter two provenances. As discussed earlier the southern provenances at age 10.5 have a much higher earlywood mean density than the more northern provenances, Figure 3.8 clearly demonstrates this. If the trend demonstrated in Figure 3.8 continues the mean earlywood densities of these provenances may converge at some future time.

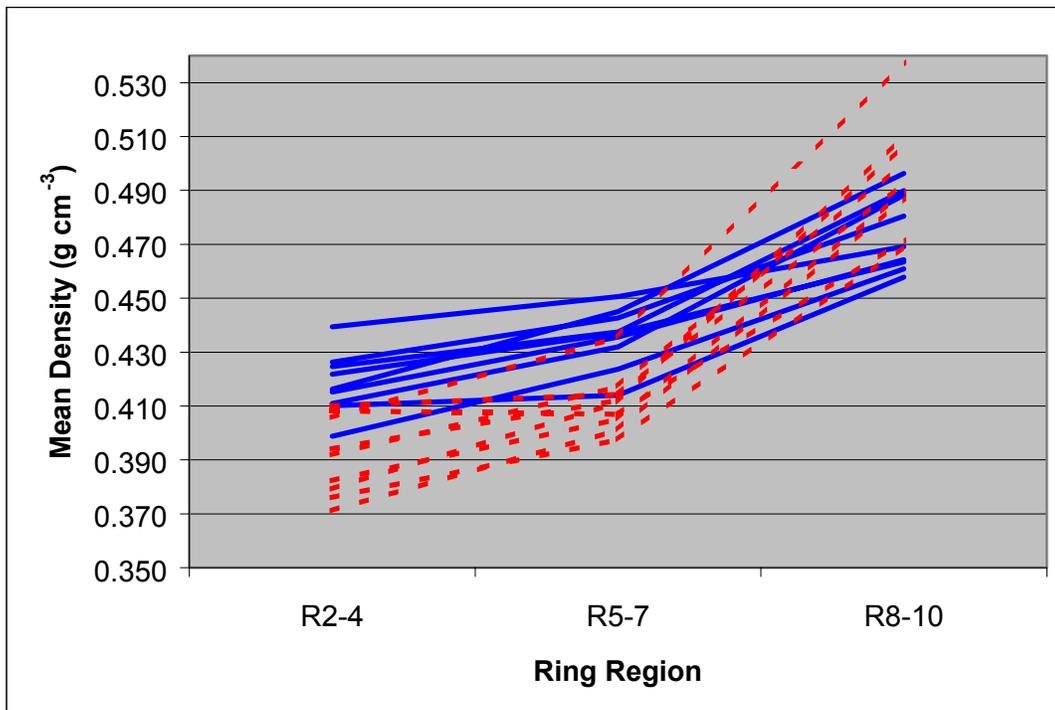
The opposite exists for mean latewood density (Figure 3.9). Potrero de Monroy and Tlacotla have a higher mean latewood density at all ages. The mean latewood density is increasing more rapidly for these two provenances and it appears that they may diverge even further from the southern provenances during the few years

of growth following sampling until they reach a maximum at some point. Given the rapid density increase in both the earlywood and latewood that has been shown, it could be expected that at some future point the overall densities of these four provenances could converge.



**Figure 3.9** Mean latewood density by ring region for four selected provenances.

The rate of increase between ring regions was investigated in more detail at the family level using family mean data from Potrero de Monroy and El Tlacuache. The detailed family data shows that families from Potrero de Monroy consistently have a more rapid increase in density between ring regions R5-7 and R8-10 than those from El Tlacuache (Figure 3.10). The trend in increase in density with age differs by provenance and the family within provenance response appears to be consistent demonstrating strong genetic control. The point of transition from juvenile to mature wood could occur earlier in families from Potrero de Monroy than families from El Tlacuache.

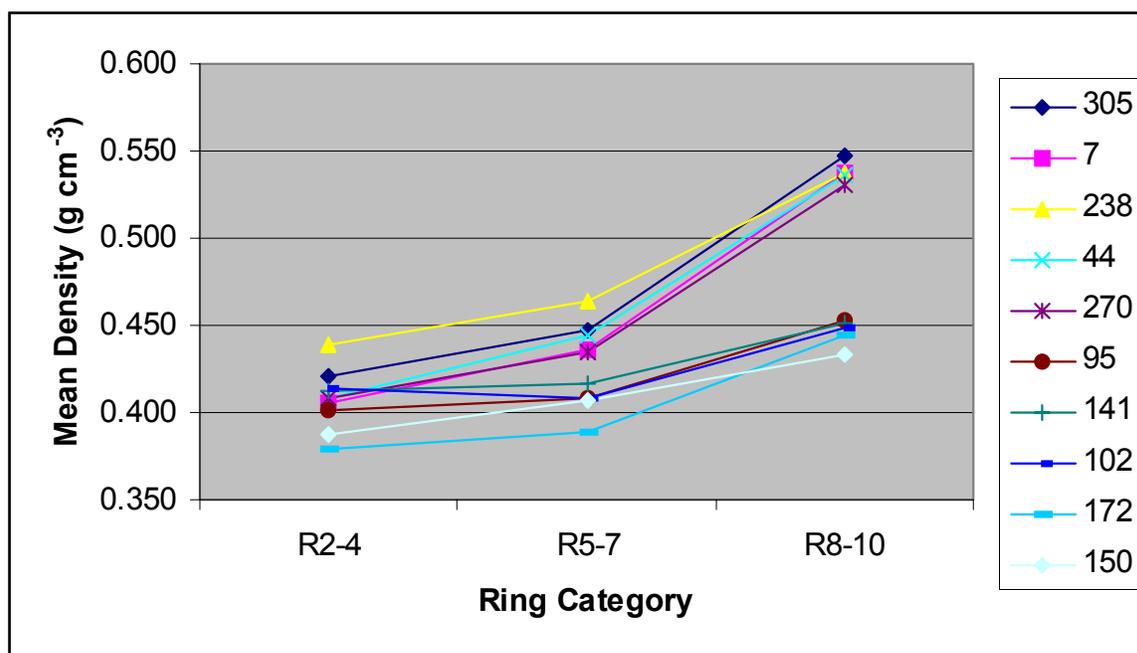


**Figure 3.10** Individual family mean density for ring regions R2-4, R5-7 and R8-10. Families (n=9) from Potrero de Monroy in red and families (n=9) from El Tlacuache in blue.

The top five and bottom five families ranked on ring category R8-10 were also plotted against mean density (Figure 3.11), the data presented in Table 3.6 confirms that differences similar to those described above are also important at the family level.

**Table 3.6** Family mean densities for core regions representing growth from the 1992-1994 (R2-4), 1995-1997 (R5-7), and 1998-2000 (R8-10) growing seasons. Top five (above dotted line) and bottom five families (below dotted line) ranked on mean density for core region R8-10.

Provenance	Family	R2-4	R5-7	R8-10
Tlacotla	305	0.420	0.448	0.547
Potrero de Monroy	7	0.406	0.436	0.538
Conrado Castillo	238	0.439	0.463	0.537
Ingenio del Rosario	44	0.408	0.445	0.536
Llano de las Carmonas	270	0.408	0.435	0.531
-----				
El Manzanal	95	0.401	0.408	0.453
Ixtlan	141	0.413	0.417	0.451
El Manzanal	102	0.414	0.408	0.449
Santa Maria Papalo	172	0.379	0.389	0.445
Ixtlan	150	0.388	0.408	0.433
Mean		0.406	0.421	0.490
SD		0.017	0.018	0.022



**Figure 3.11** Individual family mean density for ring categories R2-4, R5-7 and R8-10 for the top five and bottom five ranked families. Families ranked on mean density for ring category R8-10.

It is worth noting that four of the bottom five ranked families are from the southern provenances, El Manzanal and Ixtlan. Differences in density between the top five and bottom five families are large (Figure 3.11).

### 3.2.6 Genetic parameters

#### 3.2.6.1 Density traits

Detailed genetic parameters were calculated for all density traits (Table 3.7). The family within provenance individual heritability estimates ( $h^2_b$ ) were of a similar magnitude for weighted mean density, mean latewood density, mean earlywood density and mean percentage latewood. They ranged from 0.25 to 0.37. Similarly, the family heritability estimates ( $h^2_{f(b)}$ ) ranged from 0.45 to 0.47 with only the estimate for mean earlywood density being considerable higher (0.56).

**Table 3.7** Variance component and parameter estimates for core weighted mean density (WMD), mean earlywood density (MEWD), mean latewood density (MLWD), and percentage latewood (PLW).

	WMD	MEWD	MLWD	PLW
Mean	0.443	0.366	0.611	25.76
Variance Component				
Prov	0.000055	0.000178	0.000887	4.86
Fam(Prov)	0.000110	0.000048	0.000059	7.41
Error	0.001122	0.000345	0.000624	82.51
Parameters				
$\sigma^2_{\text{phen(prov)}}$	0.001232	0.000394	0.000683	89.93
$\sigma^2_A$	0.000329	0.000145	0.000176	22.24
$h^2_b$	0.27±0.08	0.37±0.08	0.26±0.07	0.25±0.08
$h^2_{f(b)}$	0.47	0.56	0.46	0.45
CV	0.08	0.05	0.04	0.37
GCV	0.04	0.03	0.02	0.18
$P^2_b$	0.04	0.45	1.30	0.05

These estimates are only marginally higher than typical heritability estimates for growth that are in the range 0.15 to 0.20. By direct comparison a family within provenance individual heritability ( $h^2_b$ ) of 0.20 for volume at age eight was reported for this series of South African tests (Dvorak *et al.*, 2000). The heritability estimate for mean earlywood density (0.37) was considerably higher than the estimate for weighted mean density (0.27). It may be more appropriate to select for increased earlywood density in trees grown on short pulpwood rotation as this component of overall density has a higher heritability. This option will be discussed in Chapter 7.

These heritability estimates are considerably lower than what has been reported for pines by other authors (Zobel and Jett, 1995). The reader is reminded that in this study a coefficient of relationship of 0.33 and not 0.25 was used. If 0.25 is appropriate the heritability estimates would be higher. Although many authors are vague about specific details of heritability calculation, most would probably have used a co-efficient of relationship of 0.25 for the calculation of heritability estimates from half-sib data.

Two comprehensive evaluations of the genetic variation in wood density in *P. patula* in southern Africa have reported individual heritabilities that range from 0 to 0.69 (Birks and Barnes, 1991) and 0.17 to 0.53 (Payn, 2001). In the study by Payn (2001) that included 100 half-sib families across six sites, the basic wood density of 3500 trees (cores) was determined gravimetrically. A co-efficient of relationship of 0.33 was assumed in Payn's study, so the results are directly comparable. An across site individual tree heritability of 0.29 and a family heritability of 0.38 was reported (Payn, 2001).

The heritability estimates from this study and that of Payn (2001) demonstrate that the species exhibits appreciable levels of additive variance for wood density and derived density traits, but less than what other authors have reported. Potential gains from breeding are likely to be higher if wood density or its components are also included in selection indices.

A genetic coefficient of variation (GCV) was calculated to express the genetic standard deviation as a fraction of the mean. Over cycles of selection, this can be used as a measure to determine the magnitude of genetic variation for selection (Hallauer and Miranda, 1981). For this population the GCV ranged from 2% for mean latewood density to 18% for percentage latewood (Table 3.7). This statistic indicates that sizable genetic variation exists for selection to change the percentage of latewood. The GCV can be used to compare this population with future populations that have been selected for increased wood density traits.

Provenance variance expressed as a percentage of the total phenotypic variance ( $P^2_b$ ) was moderate to high. Depending on the density trait of interest a small to large portion of the total phenotypic variance can be described in terms of the genetic parameter  $P^2_b$  (Table 3.7). For mean earlywood and latewood density the  $P^2_b$  estimates were very high, 0.45 and 1.30 respectively. For these two density traits provenance effects are very strong and important and should be taken into account in a selection and breeding strategy. This estimate indicates that provenance effects are small (4.7%) for weighted mean density.

### **3.2.6.2 Growth ring width**

Barnes *et al.* (1994) reported that ring width is under genetic control in *P. patula*, but were not able to quantify it, as only eight families were included in their study. Individual heritability estimates for growth ring width vary from 0.0 to 0.09 (Table 3.8). They are very low, an indication that growth ring width is under little or no additive genetic control. This trait therefore has little value in a breeding program.

**Table 3.8** Variance component and parameter estimates for growth rings two to ten (GRW2-GRW10).

	GRW 2	GRW 3	GRW 4	GRW 5	GRW 6	GRW 7	GRW 8	GRW 9	GRW 10
Mean	11.99	16.92	16.82	15.72	12.18	9.74	7.78	5.91	4.57
Var Component									
Prov	1.2829	0.8069	0.2185	0.1608	0.7835	0.9673	0.6135	0.6243	0.4300
Fam(Prov)	0.0000	0.0648	0.2753	0.0000	0.0294	0.2104	0.0000	0.0326	0.0941
Error	8.9683	11.4114	8.8786	8.0658	9.3472	7.2288	6.6668	3.7737	3.7082
Parameters									
$\sigma^2_{\text{phen}(\text{prov})}$	8.9683	11.4763	9.1538	8.0658	9.3766	7.4392	6.6668	3.8064	3.8023
$\sigma^2_A$	0.0000	0.1945	0.8258	0.0000	0.0882	0.6311	0.0000	0.0979	0.2824
$h^2_b$	0.00	0.02±0.07	0.09±0.06	0.00	0.01±0.05	0.08±0.06	0.00	0.03±0.05	0.07±0.06
$h^2_{f(b)}$	0.00	0.05	0.22	0.00	0.03	0.21	0.00	0.07	0.19
CV	0.25	0.20	0.18	0.18	0.25	0.28	0.33	0.33	0.43
GCV	0.00	0.03	0.05	0.00	0.02	0.08	0.00	0.05	0.12
$P^2_b$	0.14	0.07	0.02	0.02	0.08	0.13	0.09	0.16	0.11

### 3.2.6.3 Age trends

Heritability estimates for the individual core regions representing the different ages of the tree were of a similar magnitude. None was larger than the heritability estimate for whole core weighted mean density (Table 3.9). Individual heritability was highest (0.27) for the region that represents tree growth during years five to seven and then declined slightly with age.

After partitioning core regions into latewood and earlywood genetic parameters were re-calculated. Individual heritability estimates were of a similar magnitude to the estimates for the core regions that had not been partitioned (Table 3.10). A large portion of the total phenotypic variance can be described in terms of the genetic

**Table 3.9** Variance components and genetic parameter estimates for mean densities for core regions representing growth from the 1992-1994 (R2-4), 1995-1997 (R5-7), and 1998-2000 (R8-10) growing seasons. Data for weighted mean density (WMD) is repeated for comparative purposes.

	<b>WMD</b>	<b>R2-4</b>	<b>R5-7</b>	<b>R8-10</b>
Mean	0.443	0.406	0.421	0.491
Variance Component				
Prov	0.000055	0.000062	0.000093	0.000121
Fam(Prov)	0.000110	0.000093	0.000105	0.000141
Error	0.001122	0.001069	0.001061	0.002008
Parameters				
$\sigma^2_{\text{phen(prov)}}$	0.001232	0.001162	0.001166	0.002149
$\sigma^2_A$	0.000329	0.000280	0.000314	0.000422
$h^2_b$	0.27±0.08	0.24±0.08	0.27±0.08	0.20±0.07
$h^2_{f(b)}$	0.47	0.44	0.47	0.39
CV	0.08	0.08	0.08	0.09
GCV	0.04	0.04	0.04	0.04
$P^2_b$	0.04	0.05	0.08	0.06

**Table 3.10** Variance components and genetic parameter estimates for mean densities for core regions partitioned into earlywood (E) and latewood (L) representing growth from the 1992-1994 (R2-4), 1995-1997 (R5-7), and 1998-2000 (R8-10) growing seasons.

	<b>R2-4 E</b>	<b>R5-7 E</b>	<b>R8-10 E</b>	<b>R2-4 L</b>	<b>R5-7 L</b>	<b>R8-10 L</b>
Mean	0.364	0.362	0.380	0.567	0.621	0.665
Variance Component						
Prov	0.000135	0.000293	0.000121	0.000383	0.001176	0.002067
Fam(Prov)	0.000040	0.000064	0.000047	0.000022	0.000091	0.000153
Error	0.000452	0.000472	0.000447	0.000587	0.001007	0.001573
Parameters						
$\sigma^2_{\text{phen(prov)}}$	0.000492	0.000536	0.000494	0.000609	0.001098	0.001726
$\sigma^2_A$	0.000120	0.000192	0.000141	0.000065	0.000274	0.000460
$h^2_b$	0.24±0.08	0.36±0.09	0.29±0.08	0.11±0.06	0.25±0.08	0.27±0.08
$h^2_{f(b)}$	0.44	0.55	0.49	0.25	0.45	0.47
CV	0.06	0.06	0.06	0.04	0.05	0.06
GCV	0.03	0.04	0.03	0.01	0.03	0.03
$P^2_b$	0.27	0.55	0.25	0.63	1.07	1.20

parameter  $P^2_b$  (Table 3.10). For all regions of earlywood and latewood density, the  $P^2_b$  estimates were very high. Provenance effects are very strong and the importance is quantified in this statistic, confirming what can be observed in Figure 3.8 and Figure 3.9.

### 3.2.7 Phenotypic and genetic correlations

#### 3.2.7.1 Density traits

Individual tree phenotypic correlations were highly significant ( $p < 0.0001$ ) for all density traits (Table 3.11). Weighted mean density was strongly and positively correlated with mean earlywood density and percentage latewood. The correlation with mean latewood density was still positive, but weak. Family mean phenotypic correlations were of a similar magnitude and only the correlation between weighted mean density and mean latewood density was not significant. The correlations show that the important determinants of weighted mean density in juvenile trees are earlywood density and percent latewood. Density can be expected to increase with increasing earlywood density and percentage latewood.

**Table 3.11** Individual tree (above diagonal,  $n=972$ ) and family mean (below diagonal,  $n=109$ ) phenotypic correlations between density traits. Significant correlations in bold, p-values in brackets.

	WMD	MEWD	MLWD	PLW
WMD	1	<b>0.77</b> (0.000)	<b>0.13</b> (0.000)	<b>0.85</b> (0.000)
MEWD	<b>0.62</b> (0.000)	1	<b>-0.39</b> (0.000)	<b>0.74</b> (0.000)
MLWD	-0.07 (0.500)	<b>-0.78</b> (0.000)	1	<b>-0.15</b> (0.000)
PLW	<b>0.86</b> (0.000)	<b>0.78</b> (0.000)	<b>-0.40</b> (0.000)	1

More important from a tree improvement perspective are the magnitude and direction of the additive genetic correlations. All derived density traits were positively genetically correlated with weighted mean density (Table 3.12).

**Table 3.12** Additive genetic correlations with standard errors between density traits.

	WMD	MEWD	MLWD	PLW
WMD	1	0.85 ± 0.05	0.12 ± 0.20	0.95 ± 0.02
MEWD		1	-0.39 ± 0.15	0.89 ± 0.04
MLWD			1	-0.04 ± 0.21
PLW				1

The additive genetic correlations were of a similar magnitude to the phenotypic correlations, and standard errors were reasonably low (Table 3.12). The strong positive genetic correlation between earlywood density and percentage latewood is expected. As the density of the earlywood increases, a higher proportion of the total core will fall above the delineation value of 0.460 g cm<sup>-3</sup>. Based on the definition of latewood used in this study, the percentage latewood will naturally increase.

Of more interest in a breeding program is what correlated responses can be expected as a result of selection being applied to one or more of these traits. The practical implications of these correlations will be discussed in Chapter 7.

### 3.2.7.2 Growth ring width

Growth ring widths were correlated for all ages (Table 3.13). Correlation coefficients, stabilized, were of a reasonable magnitude and positive from age five (Table 3.13)

**Table 3.13** Individual tree phenotypic correlations between growth ring width (GRW) above diagonal and family mean correlations below diagonal, age two to ten. Significant correlations in bold, p-values in brackets.

	GRW 2	GRW 3	GRW 4	GRW 5	GRW 6	GRW 7	GRW 8	GRW 9	GRW 10
<b>GRW 2</b>	1	0.02 (0.689)	-0.07 (0.228)	-0.02 (0.719)	-0.09 (0.128)	<b>-0.16</b> (0.009)	<b>-0.17</b> (0.007)	<b>-0.26</b> (0.000)	<b>-0.27</b> (0.000)
<b>GRW 3</b>	<b>0.20</b> (0.039)	1	<b>0.41</b> (0.000)	<b>0.15</b> (0.000)	<b>-0.12</b> (0.002)	<b>-0.13</b> (0.000)	<b>-0.19</b> (0.000)	<b>-0.21</b> (0.000)	<b>-0.14</b> (0.000)
<b>GRW 4</b>	<b>0.19</b> (0.051)	<b>0.39</b> (0.000)	1	<b>0.48</b> (0.000)	<b>0.19</b> (0.000)	<b>0.14</b> (0.000)	0.06 (0.072)	0.04 (0.229)	0.00 (0.977)
<b>GRW 5</b>	0.03 (0.738)	0.13 (0.170)	<b>0.35</b> (0.000)	1	<b>0.45</b> (0.000)	<b>0.32</b> (0.000)	<b>0.24</b> (0.000)	<b>0.21</b> (0.000)	<b>0.14</b> (0.000)
<b>GRW 6</b>	-0.14 (0.145)	<b>-0.42</b> (0.000)	-0.06 (0.509)	<b>0.42</b> (0.000)	1	<b>0.68</b> (0.000)	<b>0.52</b> (0.000)	<b>0.50</b> (0.000)	<b>0.39</b> (0.000)
<b>GRW 7</b>	<b>-0.31</b> (0.001)	<b>-0.39</b> (0.000)	<b>-0.20</b> (0.037)	<b>0.24</b> (0.012)	<b>0.83</b> (0.000)	1	<b>0.73</b> (0.000)	<b>0.71</b> (0.000)	<b>0.54</b> (0.000)
<b>GRW 8</b>	<b>-0.23</b> (0.017)	<b>-0.37</b> (0.000)	<b>-0.30</b> (0.002)	0.11 (0.277)	<b>0.65</b> (0.000)	<b>0.81</b> (0.000)	1	<b>0.78</b> (0.000)	<b>0.62</b> (0.000)
<b>GRW 9</b>	<b>-0.29</b> (0.002)	<b>-0.45</b> (0.000)	<b>-0.29</b> (0.002)	0.13 (0.175)	<b>0.68</b> (0.000)	<b>0.82</b> (0.000)	<b>0.86</b> (0.000)	1	<b>0.74</b> (0.000)
<b>GRW 10</b>	<b>-0.26</b> (0.006)	<b>-0.33</b> (0.000)	<b>-0.27</b> (0.004)	0.11 (0.26)	<b>0.62</b> (0.000)	<b>0.75</b> (0.000)	<b>0.79</b> (0.000)	<b>0.86</b> (0.000)	1

Genetic correlations were not calculated between growth rings, these would be imprecise due to low levels of additive genetic variance, and would have little practical value.

### 3.2.7.3 Age trends

Phenotypic and additive genetic correlations between wood densities for the three core regions were all positive and highest between adjacent core regions. Standard

errors were low for the genetic correlations (Table 3.14). The lower additive genetic correlation ( $r_A = 0.59$ ) between R2-4 and R8-10 could be expected. Differences between provenances have been discussed previously. Different genes could be controlling the formation of the higher density latewood in provenances such as Potrero de Monroy and Tlacotla, or alternatively for provenances such as El Manzanal and El Tlacuache, the expression of genes controlling the formation of a more mature type of wood may have been delayed. This could account for the lower genetic correlation.

**Table 3.14** Individual tree phenotypic (above diagonal) and family mean correlations (below diagonal) between mean densities for three different core regions representing growth from the 1992-1994 (R2-4), 1995-1997 (R5-7), and 1998-2000 (R8-10) growing seasons. Significant correlations in bold, p-values in brackets.

	R2-4	R5-7	R8-10
R2-4	1	<b>0.73</b> (0.000)	<b>0.52</b> (0.000)
R5-7	<b>0.76</b> (0.000)	1	<b>0.73</b> (0.000)
R8-10	<b>0.27</b> (0.004)	<b>0.53</b> (0.000)	1

**Table 3.15** Additive genetic correlations with standard errors between three different core regions representing growth from the 1992-1994 (R2-4), 1995-1997 (R5-7), and 1998-2000 (R8-10) growing seasons.

	R2-4	R5-7	R8-10
R2-4	1	0.89 ± 0.05	0.59 ± 0.16
R5-7		1	0.79 ± 0.09
R8-10			1

After partitioning the core regions into earlywood and latewood the phenotypic and genetic correlations remained positive, strong and highest between adjacent regions within the earlywood and latewood (Table 3.16 and Table 3.17).

**Table 3.16** Individual tree phenotypic (above diagonal) and family mean correlations (below diagonal) between mean densities for three different core regions, partitioned into earlywood (E), and latewood (L) representing growth from the 1992-1994 (R2-4), 1995-1997 (R5-7), and 1998-2000 (R8-10) growing seasons. Significant correlations in bold, p-values in brackets.

	R2-4 E	R5-7 E	R8-10 E	R2-4 L	R5-7 L	R8-10 L
R2-4 E	1	<b>0.75</b> (0.000)	<b>0.63</b> (0.000)	<b>-0.25</b> (0.000)	<b>-0.24</b> (0.000)	<b>-0.25</b> (0.000)
R5-7 E	<b>0.86</b> (0.000)	1	<b>0.82</b> (0.000)	<b>-0.24</b> (0.000)	<b>-0.37</b> (0.000)	<b>-0.35</b> (0.000)
R8-10 E	<b>0.76</b> (0.000)	<b>0.90</b> (0.000)	1	<b>-0.12</b> (0.000)	<b>-0.19</b> (0.000)	<b>-0.18</b> (0.000)
R2-4 L	<b>-0.69</b> (0.000)	<b>-0.72</b> (0.000)	<b>-0.61</b> (0.000)	1	<b>0.60</b> (0.000)	<b>0.52</b> (0.000)
R5-7 L	<b>-0.61</b> (0.000)	<b>-0.76</b> (0.000)	<b>-0.64</b> (0.000)	<b>0.84</b> (0.000)	1	<b>0.71</b> (0.000)
R8-10 L	<b>-0.69</b> (0.000)	<b>-0.78</b> (0.000)	<b>-0.66</b> (0.000)	<b>0.84</b> (0.000)	<b>0.92</b> (0.000)	1

**Table 3.17** Additive genetic correlations with standard errors between three different core regions partitioned into earlywood (E) and latewood (L) representing growth from the 1992-1994 (R2-4), 1995-1997 (R5-7), and 1998-2000 (R8-10) growing seasons.

	R2-4 E	R5-7 E	R8-10 E	R2-4 L	R5-7 L	R8-10 L
R2-4 E	1	0.87 ± 0.05	0.66 ± 0.12	-0.35 ± 0.26	-0.04 ± 0.23	-0.40 ± 0.19
R5-7 E		1	0.84 ± 0.05	-0.06 ± 0.26	-0.16 ± 0.19	-0.40 ± 0.15
R8-10 E			1	-0.17 ± 0.27	-0.10 ± 0.21	-0.29 ± 0.19
R2-4 L				1	0.55 ± 0.21	0.51 ± 0.21
R5-7 L					1	0.74 ± 0.10
R8-10 L						1

Correlations between different wood types (earlywood and latewood) within and between core regions, were negative and weak. The lower genetic correlations between earlywood and latewood both within and between core regions suggests that different genes control the development of these different types of wood. The standard errors indicate that these genetic correlations are not as reliable as the estimates of genetic correlations within a wood type. A negative genetic correlation

indicates that selection to increase either the earlywood or latewood will result in a opposite response in the other trait. The magnitude and practical implications of these responses will be quantified in Chapter 7.

### 3.3 Conclusions

The results have shown that differences between provenances for all density traits are highly significant. It highlights the fact that in the absence of wood density, tree selection for growth in South Africa has concentrated on two provenances. At the age of assessment both Potrero de Monroy and Corralitla had lower wood density than average. The southern most provenances, El Tlacuache, El Manzanal, Ixtlan and Santa Maria Papalo , all classified as var. *longipedunculata*, had the highest mean earlywood density and the lowest mean latewood density. Wood from these provenances will be more uniform as the difference between latewood and earlywood density is smaller, other tracheid attributes are also likely to differ less. This may be important from a wood processing perspective.

The range in family area weighted mean density was  $0.079 \text{ g cm}^{-3}$ , this is disappointing, and will have implications for realizing genetic progress in applied breeding programs. The ranges in mean earlywood density and mean percentage latewood were greater,  $0.124 \text{ g cm}^{-3}$  and 25.64% respectively, and more encouraging.

After partitioning the core into three regions it has been shown that differences between provenances and families within provenances were highly significant for all core regions. Density trends with age indicate that some provenances such as Tlacotla and Potrero de Monroy have exhibited a rapid increase in density during the last three years of growth (years eight to ten). These provenances appear to be producing mature or transition wood earlier. Had the trees been assessed at an older age this would be likely to influence provenance rankings based on area weighted mean density.

It has been shown that a clinal pattern exists for some of the wood density traits. With the most-northern population Conrado Castillo excluded, mean earlywood density was significantly but negatively correlated ( $r = -0.90$ ) with collection site latitude. The higher density of the southern provenances of *P. patula* is driven by the density of the earlywood and not the density of the latewood. This could be age dependent and overall provenance ranking could change. On short rotations of sixteen years the density of the earlywood may be more important because it accounts for a larger proportion of the tree than the latewood.

The individual heritability estimates show that wood density is under moderate additive genetic control and therefore gains from classical breeding for general combining ability can be realized. The heritability estimate for earlywood density which is a large component of core area weighted mean density was the highest. Both the proportion and density of the earlywood play an important role and have a greater influence on whole tree density when trees are grown on short rotation pulpwood regimes. Selection for increased earlywood density may lead to a higher density more uniform raw material. Practical application of the results reported in this chapter will be discussed in Chapter 7. Growth ring width appeared to be under little to no additive genetic control, it is more likely to be influenced by environmental factors. This trait is likely to have little value in an applied breeding program.

Phenotypic and genetic correlations show that some traits are highly correlated. This data will be used in Chapter 7 to determine the magnitude of correlated responses. Standard errors of the genetic correlations indicate that they are reasonably accurate.

## Chapter 4

### Variation and Genetic Control of Tracheid Length

#### 4.1 Importance of tracheid length

Pines have a much simpler wood structure than hardwoods. The basic element in pine wood is a long narrow conductive fiber or tracheid with only about 5% or less composed of other tissues such as rays and resin canals (Burley *et al.*, 1972). The terms tracheid and fiber are both used widely in the literature, but to be technically correct the term "tracheid" should be used to describe the basic fiber in softwoods. Tracheid length affects the strength, surface and bonding properties of fiber products and is therefore of interest (Koch, 1972). It should be noted that the term tracheid length is not synonymous with the paper makers usage of the term fiber length, which is applied to processed, beaten, broken and unbroken fibers.

Quality of pine tracheids for pulp is related to the chemical constituents and the three basic dimensions of the tracheid, namely length, diameter, and cell wall thickness (Watson and Dadswell, 1961). These characteristics in turn govern such tracheid properties as flexibility and strength. Paper is formed from the collapsed and interwoven remnants of these fibrous cells of wood from which it is made. Paper therefore derives its properties from those of its constituent fibers and most particularly from the degree of inter-fiber contact or the bonding between the fibers. This is defined by the physical strength of the fibers, the degree of physical contact between them and by the degree of ionic bonding formed between adjacent fiber walls (Smook, 1992).

Very good predictions (80 percent and higher) of the properties of kraft pulp handsheets have been obtained by measurement of the primary characteristics and related properties of tracheids (Dinwoodie 1965, 1966 and Wangaard *et al.* 1966).

One of the most important fundamental fiber characteristics is its length, but investigations into its influence on pulp strength have given rise to conflicting results (Dinwoodie, 1965). In the early 1900's it was assumed that the tensile strength or breaking length and burst strength of paper were determined primarily by the length of the fiber (Dinwoodie, 1965). This misconception arose largely as a result of the use of cotton to manufacture paper. In the mid 1900's investigations showed that tracheid length does contribute to overall strength, but that the interaction of various other fiber dimensions can be more important (Dinwoodie, 1965). It is now accepted that a minimum fiber or tracheid length is required for inter-fiber bonding, and fiber length is closely related to tear strength (Zobel and van Buijtenen, 1989).

Variation in tracheid length has been related to age, rate of growth, position in tree, silvicultural treatment and growth site (Zobel and van Buijtenen, 1989; Bamber and Burley, 1983). For *P. patula* grown in Zimbabwe, it has been reported that age and site effects on tracheid length may be substantial (Muneri and Balodis, 1998). The age effect, at Stapleford, Zimbabwe, between 14 and 25-year-old trees accounted for a 25% increase in tracheid length. In comparison, the difference between sites within the same age group, expressed as a fraction of the lower value, was 13% for 14-year-old trees and 8% for 25-year-old trees (Muneri and Balodis, 1998). Ladrach (1986) has reported similar increases in tracheid length due to age for *P. patula* grown in Colombia. Environmental factors appear to be important determinants of tracheid length, perhaps even more important than genetic factors.

#### **4.2 Review of genetic control of tracheid length**

Dinwoodie (1961) in his review paper stated "*little information is available regarding the variation in tracheid length within a species in the comparison of individuals, races, provenances or forms*". Since then the variability in cell dimensions within and between trees has been quite thoroughly studied. However, results cited in the literature are often inconclusive because of design and analytical deficiencies (Zobel and Jett, 1995). In many reports it is obvious that too few families and trees per

family are used. The genetic structure of the population being studied is then not suitable for the accurate determination of genetic parameter estimates.

The inheritance of fiber length has been widely studied, particularly in hardwoods because it is often considered to be a limiting factor in their use. In hardwoods most fibers are less than 2 mm in length (Zobel and Jett, 1995) and the value of an improvement is often questioned. Zobel and Jett (1995) cite other authors who have reported heritabilities in the range 0.32 to 0.52 for *Eucalyptus* species and broad sense heritabilities of 0.36 to 0.86 in the genus *Populus*.

In the pines, heritabilities have been reported to be high and variation large for tracheid length, indicating that good genetic gains are possible. Reported heritabilities range from 0.01 to 0.97, but it has been generally accepted that tracheid length is under moderate genetic control (Zobel and Jett, 1995). Barnes *et al.* (1994) concluded that tracheid length was under genetic control in *P. patula* and that juvenile-mature correlations were strong; tracheid length at seven years can be predicted very precisely by measuring the trait in any of the rings laid down from the third to the seventh years. Correlations at the family level between tracheid length at breast height of individual rings one to six and weighted tracheid length for the whole disc at breast height ranged from 0.72 to 0.99, and were influenced by site (Barnes *et al.*, 1994).

Concerns about the validity of some of the published results have been raised, particularly when a limited number of provenances and families are studied (Zobel and Jett, 1995). In one of the earliest studies that reports on the inheritance of tracheid length in pines, measurements were made on tracheids from the wood in the first ring from the pith of branches of ten open-pollinated and seven control-pollinated families and their parents (Jackson and Greene, 1958). Ten progeny and the parents were evaluated from each family. Data from this study did not permit the calculation of any quantitative parameters such as a heritability estimate,

nevertheless it was concluded that tracheid length was under strong genetic control (Jackson and Greene, 1958).

Nicholls (1967) reported that clonal heritability values for tracheid length are subject to a pattern of change with increasing age, increasing from the pith until a maximum of 0.50 is reached at about the fifth to ninth ring from the pith and then declining to a value of 0.20 in subsequent growth rings. In Nicholls's (1967) study, three trees from 19 *P. radiata* clones were sampled. Each sample was represented by 22 growth rings. No conclusions with regard to the magnitude of additive genetic variance can be made. The narrow sense or individual tree heritabilities estimates are, of course, likely to be lower than the clonal heritabilities.

Cown *et al.* (1992) sampled 30 open-pollinated *P. radiata* families in New Zealand, the number of trees sampled per family varied from nine to 15, but averaged 11. The outermost two complete growth rings were removed from the 10 mm cores, and macerated. Trees within families were bulked (Cown *et al.* 1992). A between family co-efficient of variation of 3.5% was reported suggesting a family heritability of 0.7 (Cown *et al.* 1992).

In a study in east Texas, wood samples were collected from a 25-year-old loblolly pine open-pollinated test planted at two locations (Loo *et al.*, 1984). Fifteen families and five trees per family were sampled. Differences between families for tracheid length were not significant and heritability estimates for tracheid length of loblolly pine grown in east Texas were found to be low at all ages (Loo *et al.*, 1984). The individual tree heritability estimates for tree ages two to ten varied from 0.0 to a maximum of 0.15, similarly family mean heritabilities ranged from 0.0 to 0.32 (Loo *et al.*, 1984). Standard errors for the estimates were however, large. Loo *et al.* (1984) concluded that tracheid length may be under little genetic control, but there is an apparent age dependency and tracheid length can probably not be changed easily by selection.

The major unknown is the economic worth of changes obtained from the genetic manipulation of tracheid length. Tracheid length may be particularly important in pines grown in the tropics, as tracheids in the juvenile wood are shorter, and even a small increase may have a significant effect on pulp and paper quality. Greater tracheid length has been related to improvements in burst, tear and tensile strength, but these have varying levels of importance depending on the end product.

This chapter will report on the variation and genetic control of tracheid length in 10.5-year-old *P. patula* grown in South Africa.

### 4.3 Results and discussion

#### 4.3.1 Pith-to-bark trends

For all five rings and mean tree ages, residuals were plotted against fitted values, and showed no detectable trends or patterns. It can therefore be said that the conditions that  $\varepsilon_{ijk} \sim \text{iid}(0, \sigma^2)$  have been met for this data and the standard ANOVA assumptions, are valid. Simple statistics were calculated for tracheid length for each ring assessed (Table 4.1).

**Table 4.1** Mean, standard deviations (SD), minimum, maximum, median and mode in millimetres for individual tree tracheid length at 1.2 m above ground level from rings two, four, six, eight and ten.

Variable	n (N=998)	Mean (mm)	SD (mm)	Minimum (mm)	Maximum (mm)	Median (mm)	Mode <sup>1</sup> (mm)
Ring 2	894	1.58	0.202	1.18	2.85	1.54	1.4 - 1.6
Ring 4	994	2.00	0.217	1.15	3.10	1.98	1.8 - 2.0
Ring 6	996	2.72	0.287	1.88	3.90	2.70	2.6 - 2.8
Ring 8	996	3.51	0.291	2.26	4.66	3.50	3.4 - 3.6
Ring 10	993	4.25	0.383	3.06	5.44	4.32	4.4 - 4.6

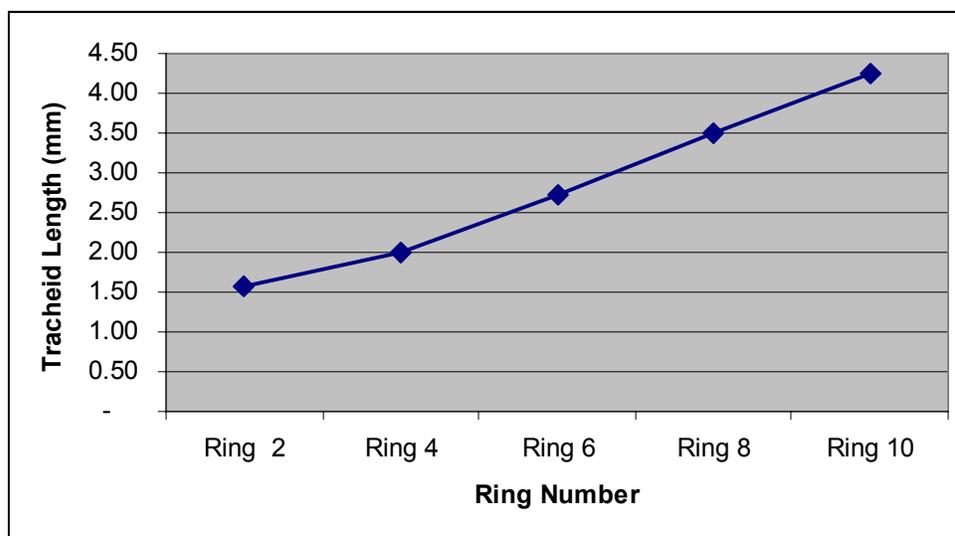
<sup>1</sup> mode is defined as the 0.2mm class with the highest frequency (see Figure 4.2).

For 104 samples (out of N=998 including controls) data were not available for ring two. It is likely that the pith was missed when the core was removed from these trees and the inner most growth ring at breast height was therefore not sampled. For the remaining rings, a few outlier data points were deleted prior to analysis (Table 4.1).

In an earlier study in South Africa, Wright and Sluis-Cremer (1992) reported mean tracheid lengths of 2.40 mm and 2.90 mm for rings four and eight respectively. The estimates obtained in this study are similar for the same rings (Table 4.1). Based on breast height samples taken from 27-year-old *P. patula* grown in Tanzania, Ishengoma *et al.* (1995) reported a mean tracheid length of 2.56 mm for juvenile wood of *P. patula*. Juvenile wood was defined as being comprised of the first eight rings from the pith. In this study the un-weighted tracheid mean length for the first eight rings was 2.46 mm.

It is well known that tracheid length increases dramatically in a radial direction during the first 10 years of a pine trees growth. These data show that the mean tracheid length of *P. patula* increases nearly three fold from ring two (1.58 mm) through to ring ten (4.25 mm), see Figure 4.1. Barnes *et al.* (1994) report similar ranges in mean tracheid length for seven and a half year old *P. patula* grown on two sites in Zimbabwe, although the increase from pith-to-bark appears to be more rapid. In the Zimbabwean study, mean tracheid length was already in the range 3.50 mm to 4.40 mm at age seven. Ringo and Klem (1989) in a study conducted on thirty trees from a 27-year-old *P. patula* plantation in southern Tanzania reported an increase in mean tracheid length from 2.22 mm for ring two to 3.06 mm for ring ten. Lubomir (1969) studied tracheid length in *P. patula* grown in Tanzania. Trees ranging in age from 11 to 22 collected from six different sites were sampled. The radial increase in tracheid length were reported to range from 2.20 mm for an age two tree to 3.60 mm for an age ten tree. Unfortunately, Lubomir (1969) does not describe in any detail how samples were measured, but reports only averages for each site. A mean tracheid length of 4.20 mm has been reported for ten-year-old *P. patula* grown in Colombia

(Ladrach, 1984). Despite limited literature on the variation in tracheid length in *P. patula* most studies reported are in agreement with general trends and ranges. Barnes *et al.* (1994) did demonstrate that site can have an effect on tracheid length. Therefore direct comparisons with other studies cannot be made but reported tracheid lengths in Zimbabwe are similar to those found for the data in this study.

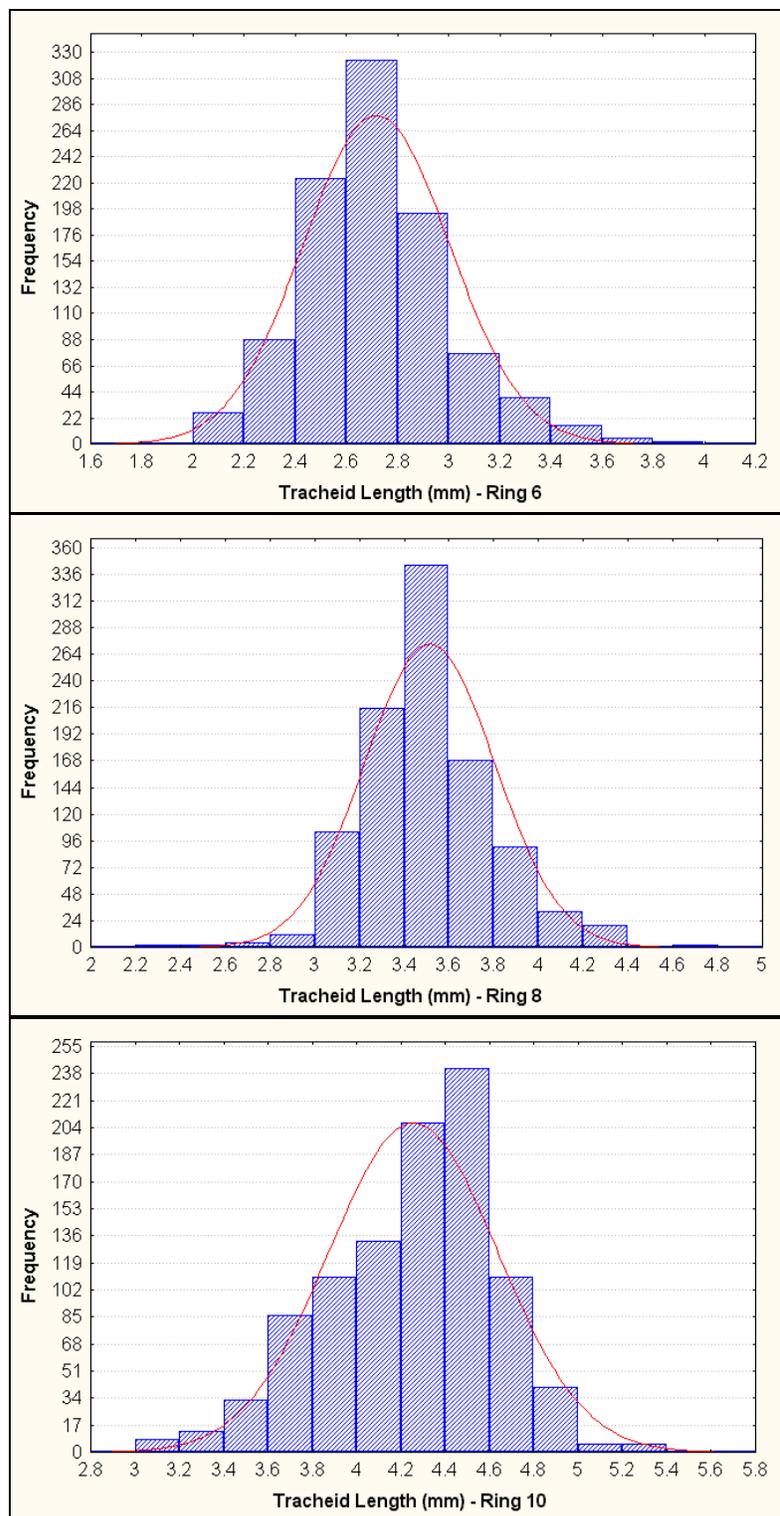


**Figure 4.1** Pith-to-bark variation in tracheid length, mean of approximately 998 trees (Table 4.1).

Muneri and Balodis (1998) concluded that the period of rapid increase in tracheid length is about eight growth rings in *P. patula*. It is possible therefore that in subsequent growth rings (after ring 10), that the steep ring to ring increase in tracheid length would not continue (Figure 4.1). Radial trends in tracheid length found in this study conform with those previously reported.

#### 4.3.2 Within ring tracheid length distribution.

The distribution of mean tracheid length was investigated on an individual tree basis for all five rings. For ring two to ring eight the distribution was normal, only for tracheid length in ring ten was the distribution skewed slightly (Figure 4.2). For all other rings the mean tracheid length for the ring fell within the same range as the



**Figure 4.2** Individual tree mean tracheid length distribution for rings six, eight and ten.

mode (Table 4.1). The frequency distribution of tracheid length is what would be expected from a metric character.

### 4.3.3 Provenance variation

No reports could be found in the literature on the magnitude of provenance variation for tracheid length in *P. patula*. Results from this study show that differences between provenances were highly statistically significant ( $P < 0.01$ ) for individual ring tracheid length, and mean tracheid length at different ages (Appendix 5). The local South African control had consistently longer tracheid length for rings four, six, eight and ten while Conrado Castillo had the shortest tracheids (Table 4.2).

**Table 4.2** Provenance mean tracheid length at 1.2 m above ground from rings two, four, six, eight and 10, ranked on mean tracheid length for ring 10.

Provenance	Ring 2 (mm)	R <sup>1</sup>	Ring 4 (mm)	R	Ring 6 (mm)	R	Ring 8 (mm)	R	Ring 10 (mm)	R
SA control	1.61	4	2.10	1	2.81	1	3.62	1	4.37	1
Zacualtipan	1.55	12	2.00	6	2.76	3	3.60	2	4.33	2
Ingenio del Rosario	1.68	1	2.08	2	2.76	4	3.52	5	4.33	3
Tlacotla	1.61	5	2.04	4	2.76	5	3.59	3	4.29	4
Santa Maria Papalo	1.56	10	1.98	10	2.68	10	3.48	10	4.28	5
Pinal de Amoles	1.56	8	1.99	8	2.68	11	3.48	11	4.26	6
El Tlacuache	1.63	2	2.05	3	2.72	7	3.52	6	4.26	7
Ixtlan	1.61	6	1.99	7	2.73	6	3.55	4	4.24	8
Llano de las Carmonas	1.55	11	1.96	12	2.77	2	3.49	9	4.23	9
Corralitla	1.56	9	1.97	11	2.70	8	3.50	7	4.22	10
Potrero de Monroy	1.59	7	2.02	5	2.67	12	3.50	8	4.22	11
El Manzanal	1.62	3	1.98	9	2.69	9	3.47	12	4.21	12
Conrado Castillo	1.54	13	1.92	13	2.65	13	3.43	13	4.14	13
Mean	1.58		2.00		2.72		3.52		4.25	
SD	0.04		0.05		0.05		0.05		0.06	
Minimum	1.54		1.92		2.65		3.43		4.14	
Maximum	1.68		2.10		2.81		3.62		4.37	
Range	0.14		0.18		0.24		0.19		0.23	

<sup>1</sup> Provenance rank.

Corralitla and Potrero de Monroy tended to have shorter tracheids than average, these two provenances also tended to have lower wood density values. Conrado Castillo which was the top ranked provenance for wood density, consistently had the shortest tracheids across all rings. Possible correlations between wood density traits, tracheid length, and tracheid cross-sectional properties will be investigated in Chapter 6. Although the differences between provenances were statistically significant the magnitude of these differences is unlikely to be of any practical value. The consistency of ranking between age six, age eight and age 10 (Table 4.3) shows that provenance mean tracheid length can be assessed at a relatively young age. Later in this chapter, phenotypic and additive genetic correlations will be discussed in more detail.

**Table 4.3** Provenance mean tracheid length at 1.2 m above ground for ages two to age ten, ranked on mean tracheid length for an age 10 tree.

Provenance	Age 2 (mm)	R <sup>1</sup>	Age 4 (mm)	R	Age 6 (mm)	R	Age 8 (mm)	R	Age 10 (mm)	R
SA control	1.61	4	1.87	2	2.20	1	2.57	1	2.93	1
Ingenio del Rosario	1.68	1	1.88	1	2.18	2	2.52	2	2.88	2
Tlacotla	1.61	5	1.83	4	2.15	4	2.51	3	2.87	3
Zacualtipan	1.55	12	1.77	9	2.10	8	2.48	6	2.85	4
El Tlacuache	1.63	2	1.86	3	2.15	3	2.49	4	2.84	5
Ixtlan	1.61	6	1.81	7	2.13	5	2.49	5	2.84	6
El Manzanal	1.62	3	1.82	5	2.13	6	2.47	7	2.82	7
Potrero de Monroy	1.59	7	1.81	6	2.11	7	2.46	8	2.81	8
Llano de las Carmonas	1.55	11	1.76	12	2.10	9	2.45	9	2.81	9
Santa Maria Papalo	1.56	10	1.77	11	2.08	12	2.43	12	2.81	10
Pinal de Amoles	1.56	8	1.78	8	2.09	11	2.44	11	2.81	11
Corralitla	1.56	9	1.77	10	2.09	10	2.45	10	2.80	12
Conrado Castillo	1.54	13	1.74	13	2.04	13	2.39	13	2.74	13
Mean	1.58		1.79		2.10		2.46		2.83	
SD	0.04		0.04		0.04		0.04		0.04	
Minimum	1.54		1.74		2.04		2.39		2.74	
Maximum	1.68		1.88		2.20		2.57		2.93	
Range	0.14		0.14		0.16		0.18		0.19	

<sup>1</sup> Provenance rank.

Provenance rank changes between tracheid length evaluated on an individual ring basis (Table 4.2) and an age basis (Table 4.3) were minor and are unlikely to alter any conclusions that would be drawn from the data.

#### 4.3.4 Family variation

Differences between families within provenances were only significant ( $P < 0.05$ ) for tracheid length from rings six and ten and were not significant for any of the other respective ages (Appendix 5). This result was surprising. Zobel and Jett (1995) draw the conclusion that tracheid length is under "*moderate genetic control*". Given the large number (108) of half-sib families in this study between family variation would be expected to be apparent. This aspect will be discussed in more detail in the section on genetic parameters.

For all rings and ages, the difference between the best and worst family did not exceed 0.50 mm, this range of variation in family means is unlikely to be of practical significance, or usable in an applied breeding program (Table 4.4 and Table 4.5). Barnes *et al.* (1994) report on similar orders of difference between the best and worst families, however they only worked with six control pollinated families and two open-pollinated commercial checks. Cown *et al.* (1992) reported that for 30 *P. radiata* families average tracheid length ranged from 3.36 to 3.97 mm. Given the large number of families in this study, and their diverse genetic background, a larger range in family mean tracheid length was expected. It appears as if most of the variation is at the individual tree level, the range between the best and worst tree for each ring is in the region of 2.0 mm (Table 4.1). This indicates that variation in tracheid length at the individual tree level may be due to environmental factors or gene action. It may be that non-additive gene action or epistatic effects are important determinants of tracheid length.

Family ranking based on mean ring tracheid length was inconsistent between rings (Table 4.4). From a practical perspective, this means that family tracheid length cannot be accurately predicted by a sample taken from a specific ring. Family ranking across the range of ages in this study was more consistent, but the greater the difference in age the less consistent the ranking was (Table 4.5).

**Table 4.4** Top ten (above dotted line) and bottom ten ranked families for mean tracheid length at 1.2 m above ground from ring 10 and mean tracheid length for the same families from rings two, four, six and eight.

Family	Provenance	Ring 2 (mm)	R <sup>1</sup>	Ring 4 (mm)	R <sup>1</sup>	Ring 6 (mm)	R <sup>1</sup>	Ring 8 (mm)	R <sup>1</sup>	Ring 10 (mm)	R <sup>1</sup>
160	Santa Maria Papalo	1.60	44	1.86	105	2.64	85	3.47	73	4.49	1
252	Zacualtipan	1.53	87	1.99	59	2.78	28	3.66	8	4.49	2
51	Ingenio del Rosario	1.74	3	2.19	1	2.79	25	3.50	57	4.47	3
50	Ingenio del Rosario	1.51	97	2.03	38	2.80	19	3.68	4	4.46	4
163	Santa Maria Papalo	1.52	92	2.00	56	2.75	46	3.57	27	4.45	5
262	Zacualtipan	1.60	45	2.06	28	2.95	1	3.67	5	4.44	6
38	Ingenio del Rosario	1.73	5	2.03	41	2.71	60	3.53	43	4.43	7
268	Llano de las Carmonas	1.58	56	2.01	47	2.90	3	3.63	13	4.42	8
167	Santa Maria Papalo	1.56	65	1.93	92	2.52	105	3.42	93	4.41	9
301	Tlacotla	1.71	7	2.00	55	2.81	16	3.58	25	4.41	10
225	Conrado Castillo	1.49	103	1.99	62	2.68	77	3.42	92	4.11	99
125	El Tlacuache	1.60	40	1.99	64	2.61	92	3.40	100	4.10	100
169	Santa Maria Papalo	1.56	73	2.02	45	2.81	15	3.41	98	4.09	101
53	Ingenio del Rosario	1.67	13	1.98	66	2.72	59	3.46	78	4.08	102
22	Potrero de Monroy	1.63	25	2.12	5	2.77	29	3.53	44	4.07	103
159	Santa Maria Papalo	1.52	91	1.87	102	2.55	103	3.34	107	4.07	104
241	Conrado Castillo	1.63	33	1.96	79	2.73	52	3.48	63	4.07	105
230	Conrado Castillo	1.49	105	1.93	93	2.75	43	3.40	101	4.06	106
280	Llano de las Carmonas	1.55	79	1.84	108	2.75	39	3.53	42	4.04	107
227	Conrado Castillo	1.51	96	1.88	101	2.57	100	3.36	106	4.02	108
	Mean	1.58		2.00		2.72		3.52		4.25	
	SD	0.07		0.07		0.10		0.09		0.11	
	Minimum	1.42		1.81		2.44		3.30		4.02	
	Maximum	1.77		2.19		2.95		3.74		4.49	
	Range	0.35		0.38		0.51		0.44		0.47	

<sup>1</sup> Family rank out of 108 families

Family ranking was not consistent across rings and between rings and different age trees. Only three families that appeared in the top rankings based on mean tracheid length for ring ten also appeared in the top ranked families when ranked on mean tracheid length for an age ten tree. Phenotypic and additive genetic correlations between traits are discussed in more detail later in this chapter.

**Table 4.5** Top ten (above dotted line) and bottom ten ranked families for mean tracheid length at 1.2 m above ground for an age 10 tree and mean tracheid length for the same families from age two, four, six and eight.

Family	Provenance	Age 2 (mm)	R <sup>1</sup>	Age 4 (mm)	R <sup>1</sup>	Age 6 (mm)	R <sup>1</sup>	Age 8 (mm)	R <sup>1</sup>	Age 10 (mm)	R <sup>1</sup>
119	El Tlacuache	1.77	1	1.98	1	2.29	1	2.63	1	2.97	1
51	Ingenio del Rosario	1.74	3	1.98	2	2.26	2	2.58	3	2.95	2
262	Zacuatlipan	1.60	44	1.81	46	2.19	12	2.57	6	2.94	3
45	Ingenio del Rosario	1.72	6	1.91	5	2.23	3	2.57	5	2.93	4
80	El Manzanal	1.59	49	1.80	52	2.16	24	2.56	7	2.92	5
305	Tlacotla	1.70	8	1.84	28	2.16	25	2.54	15	2.92	6
147	Ixtlan	1.75	2	1.92	3	2.22	5	2.55	9	2.91	7
268	Llano de las Carmonas	1.58	55	1.80	53	2.17	21	2.53	16	2.91	8
309	Tlacotla	1.64	22	1.87	18	2.20	9	2.57	4	2.91	9
295	Tlacotla	1.66	17	1.91	6	2.22	4	2.58	2	2.91	10
230	Conrado Castillo	1.49	104	1.72	99	2.07	80	2.41	84	2.75	99
125	El Tlacuache	1.60	39	1.83	33	2.08	75	2.41	88	2.74	100
26	Potrero de Monroy	1.50	101	1.72	95	2.01	98	2.36	102	2.74	101
225	Conrado Castillo	1.49	102	1.75	83	2.06	87	2.40	94	2.73	102
159	Santa Maria Papalo	1.52	90	1.72	96	2.03	97	2.37	101	2.73	103
63	Corralitla	1.53	88	1.68	107	1.97	107	2.35	106	2.71	104
67	Corralitla	1.42	108	1.68	106	1.99	104	2.35	104	2.71	105
228	Conrado Castillo	1.52	92	1.71	102	1.99	105	2.35	105	2.70	106
238	Conrado Castillo	1.52	94	1.66	108	1.94	108	2.28	108	2.70	107
227	Conrado Castillo	1.51	95	1.69	105	1.98	106	2.32	107	2.66	108
	Mean	1.58		1.79		2.10		2.46		2.83	
	SD	0.07		0.06		0.07		0.06		0.06	
	Minimum	1.42		1.66		1.94		2.28		2.66	
	Maximum	1.77		1.98		2.29		2.63		2.97	
	Range	0.35		0.32		0.35		0.35		0.31	

<sup>1</sup> Family rank out of 108 families

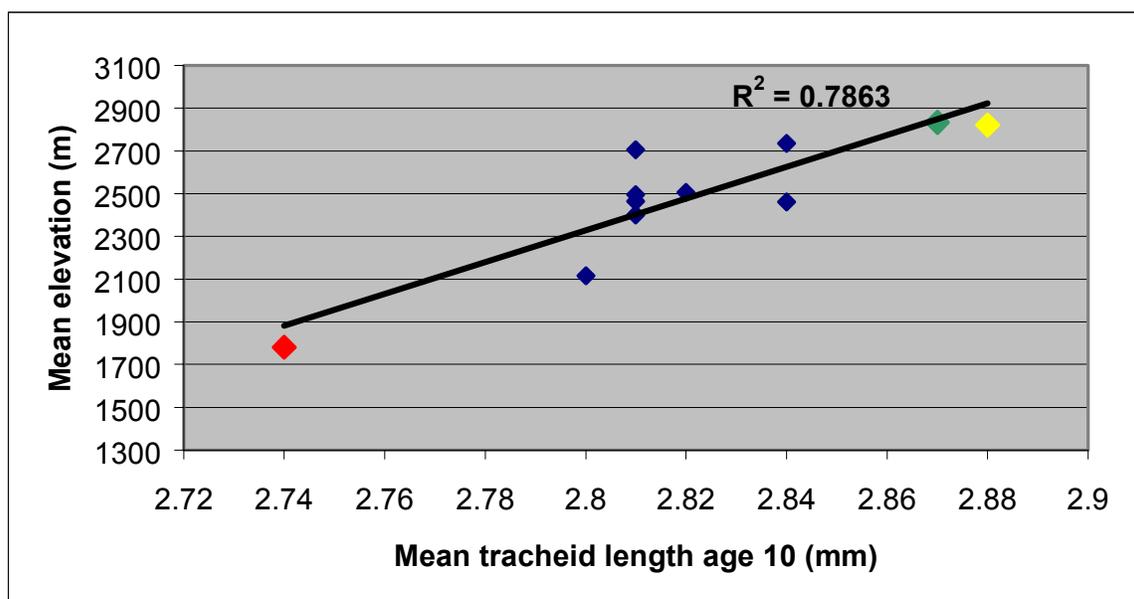
### 4.3.5 Correlation with collection sites

In the preceding chapter, the existence of a clinal pattern for density traits was demonstrated. It raised the question whether clinal patterns existed for the other wood properties. Provenance mean ring and mean age tracheid length were correlated with collection site climatic data as outlined in the materials and methods. Zacualtipán was identified as an outlier provenance and was not included in the data set when the correlations were calculated (Table 4.6).

**Table 4.6** Correlation of mean age tracheid length and mean ring tracheid length for ages two, four, six, eight and 10 years with collection site latitude, longitude, mean annual precipitation (MAP), mean annual precipitation (MAP) and mean elevation (Elav.). Significant correlations in bold, p-values in brackets.

<b>Zacualtipan excluded</b>					
<b>Variable</b>	<b>Lat. (N)</b>	<b>Long. (W)</b>	<b>MAP (mm)</b>	<b>MAT (°C)</b>	<b>Elev. (m)</b>
Age 2	-0.47 (0.149)	-0.45 (0.170)	0.04 (0.901)	-0.36 (0.272)	0.59 (0.054)
Age 4	-0.47 (0.141)	-0.37 (0.268)	0.06 (0.864)	-0.30 (0.378)	<b>0.61</b> (0.048)
Age 6	-0.54 (0.087)	-0.46 (0.157)	0.07 (0.830)	-0.35 (0.288)	<b>0.78</b> (0.005)
Age 8	-0.52 (0.099)	-0.45 (0.160)	0.13 (0.696)	-0.35 (0.296)	<b>0.81</b> (0.003)
Age 10	-0.51 (0.106)	-0.44 (0.175)	0.01 (0.970)	-0.32 (0.330)	<b>0.89</b> (0.000)
<b>Variable</b>	<b>Lat. (N)</b>	<b>Long. (W)</b>	<b>MAP (mm)</b>	<b>MAT (°C)</b>	<b>Elev. (m)</b>
Ring 2	-0.47 (0.149)	-0.45 (0.170)	0.04 (0.901)	-0.36 (0.272)	0.59 (0.054)
Ring 4	-0.34 (0.302)	-0.22 (0.510)	0.03 (0.940)	-0.33 (0.328)	<b>0.65</b> (0.029)
Ring 6	-0.30 (0.363)	-0.35 (0.294)	0.02 (0.954)	-0.53 (0.094)	<b>0.79</b> (0.004)
Ring 8	-0.37 (0.265)	-0.29 (0.380)	0.15 (0.652)	-0.26 (0.432)	<b>0.73</b> (0.011)
Ring 10	-0.37 (0.258)	-0.32 (0.342)	-0.08 (0.825)	-0.25 (0.458)	<b>0.79</b> (0.004)

Only the mean elevation of collection sites was significantly correlated with tracheid length at both the ring and mean tree age level. These correlations were positive and significant ( $P < 0.05$ ) (Table 4.6). This seems to indicate that elevation of collection site is important, with Conrado Castillo the most northern and lowest elevation site having the shortest tracheids. Mean collection site elevation was plotted against mean tracheid length at age 10 (Figure 4.3), the age with the strongest correlation ( $r = 0.89$ ).



**Figure 4.3** Mean tracheid length at age 10 plotted against provenance collection site mean elevation, Zacualtipán excluded, demonstrating the effect of altitude on tracheid length.

From Figure 4.3 it can be seen that three provenances, Conrado Castillo (red), Ingenio del Rosario (green) and Tlacotla (yellow), have a major influence on the correlation. This could be biasing the correlation. A true correlation between tracheid length and mean elevation of collection site may not exist.

### 4.3.6 Genetic parameters

Detailed genetic parameters were calculated (Table 4.7) using the methods described in Chapter 2. Depending on ring number, the family within provenance individual heritability ( $h^2_b$ ) varied from 0.0 to 0.13 (Table 4.7).

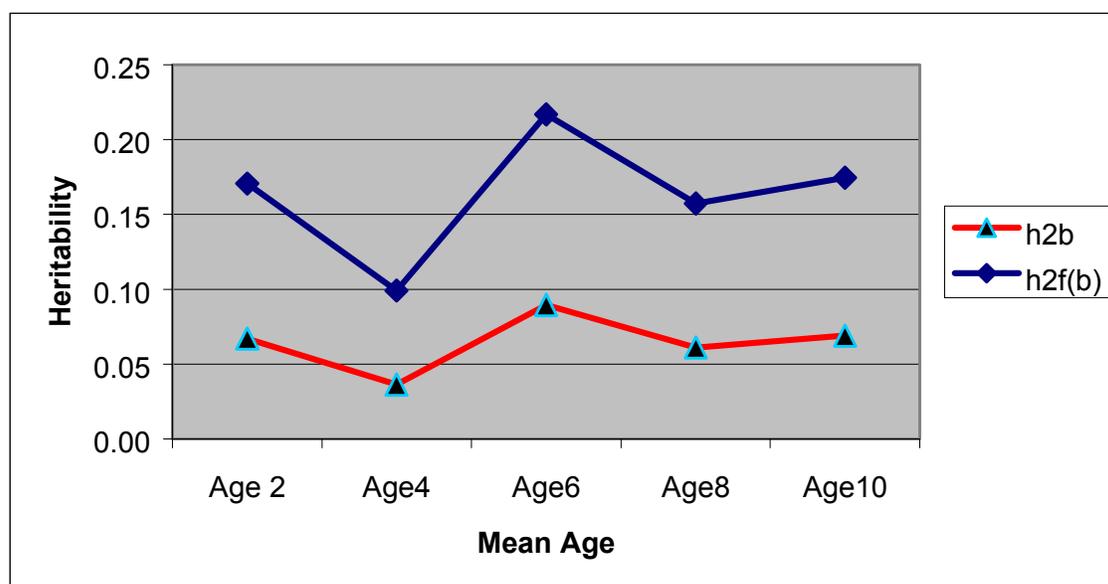
**Table 4.7** Genetic parameters on a ring by ring and age within core basis.

	Ring 2	Ring 4	Ring 6	Ring 8	Ring 10
Mean	1.58 mm	2.00 mm	2.72 mm	3.51 mm	4.25 mm
Variance Component					
Prov	0.000673	0.000909	0.000000	0.000758	0.001307
Fam(Prov)	0.000509	0.000849	0.002870	0.000000	0.002270
Error	0.022270	0.036530	0.061640	0.065050	0.066240
Parameters					
$\sigma^2_{\text{phen(prov)}}$	0.022779	0.037379	0.064510	0.065050	0.068510
$\sigma^2_A$	0.001527	0.002547	0.008610	0.000000	0.006810
$h^2_b$	0.07±0.065	0.07±0.059	0.13±0.065	0.00	0.10±0.063
$h^2_{f(b)}$	0.17	0.17	0.30	0.00	0.24
CV	0.10	0.10	0.09	0.07	0.06
GCV	0.02	0.03	0.03	0.00	0.02
$P^2_b$	0.03	0.02	0.00	0.01	0.02
	Age 2	Age 4	Age 6	Age 8	Age 10
Mean	1.58 mm	1.79 mm	2.10 mm	2.45 mm	2.81 mm
Variance Component					
Prov	0.000673	0.001051	0.000574	0.000580	0.000663
Fam(Prov)	0.000509	0.000243	0.000652	0.000437	0.000455
Error	0.022270	0.019870	0.021200	0.021070	0.019360
Parameters					
$\sigma^2_{\text{phen(prov)}}$	0.022779	0.020113	0.021852	0.021507	0.019815
$\sigma^2_A$	0.001527	0.000729	0.001956	0.001311	0.001365
$h^2_b$	0.07±0.065	0.04±0.060	0.09±0.065	0.06±0.062	0.07±0.063
$h^2_{f(b)}$	0.17	0.10	0.22	0.16	0.17
CV	0.10	0.08	0.07	0.06	0.05
GCV	0.02	0.02	0.02	0.01	0.01
$P^2_b$	0.03	0.05	0.03	0.03	0.03

These estimates were much lower than expected. The standard errors were of a similar magnitude to the estimates themselves. Similarly, the family heritability ( $h^2_{f(b)}$ ) varied from 0.0 to 0.30. These estimates demonstrate that the species exhibits very low levels of additive genetic control for tracheid length, and potential gains from conventional breeding are likely to be low.

A genetic coefficient of variation (GCV) was calculated to express the genetic standard deviation as a fraction of the mean. Over cycles of selection, this can be used as measure to determine the magnitude of genetic variation for selection. For this population, the GCV ranged from 0 to 3%. This provides another indication that levels of additive genetic variation for selection are very low.

Heritability estimates for tracheid length at various ages were also low, ranging from 0.04 to 0.09 for individual heritabilities and 0.10 to 0.22 for family heritabilities (Table 4.7; Figure 4.4).



**Figure 4.4** Tracheid length, individual and family within provenance heritability trend with age.

Age trends (Figure 4.4) were similar to those reported by Loo *et al.* (1984) for loblolly pine grown in east Texas. In the Texas study for ages two to ten individual heritability estimates ranged from 0.0 to 0.15 and family heritabilities from 0.0 to 0.32 (Loo *et al.*, 1984). Both results indicate that although tracheid length is under weak additive genetic control, it may be age dependent. Nicholls (1967) also reported a similar age trend in clonal heritability determined using tracheid length data from nineteen *P. radiata* clones in South Australia. Although the clonal heritability estimates were higher, they appeared to peak at growth ring seven and then declined to flatten at 0.20 from growth ring 13. Heritability estimates peaked at age six in this study (Figure 4.4).

Provenance variance expressed as a percentage of the total phenotypic variance ( $P^2_b$ ) was very low ranging from zero to five percent. Only a very small portion of the total phenotypic variance for tracheid length can be described in terms of the genetic parameters in Table 4.7. Environmental factors that cannot be predicted from this data seem to play a significant role in determining tracheid length.

### **4.3.7 Phenotypic and additive genetic correlations**

#### **4.3.7.1 Ring - ring correlations**

Ring-ring phenotypic correlations were calculated on individual tree values and family means. Within individual tree ring-ring or radial pith-to-bark tracheid length correlations were low (Table 4.8). In some cases where rings are relatively far apart, the correlation coefficients were even negative. With the exception of the correlation between ring two and ring eight, the family mean correlations were statistically significant (Table 4.8), but remained low and appear to have limited practical application other than providing some indication of what could be expected from the adjacent rings.

**Table 4.8** Within individual tree ring-ring phenotypic correlation coefficients for tracheid length above diagonal (n=972), and family mean ring-ring phenotypic correlations (n=109) below diagonal. Significant correlations in bold, p-values in brackets.

	Ring 2	Ring 4	Ring 6	Ring 8	Ring 10
Ring 2	1	<b>0.57</b> (0.000)	<b>0.27</b> (0.000)	-0.03 (0.342)	<b>-0.37</b> (0.000)
Ring 4	<b>0.60</b> (0.000)	1	<b>0.55</b> (0.000)	<b>0.28</b> (0.000)	<b>-0.08</b> (0.010)
Ring 6	<b>0.28</b> (0.003)	<b>0.58</b> (0.000)	1	<b>0.54</b> (0.000)	<b>0.10</b> (0.002)
Ring 8	<b>0.15</b> (0.113)	<b>0.37</b> (0.000)	<b>0.62</b> (0.000)	1	<b>0.41</b> (0.000)
Ring 10	<b>0.25</b> (0.010)	<b>0.29</b> (0.002)	<b>0.27</b> (0.005)	<b>0.48</b> (0.000)	1

Due to the low individual and family correlations provenance mean phenotypic correlations were calculated (Table 4.9).

**Table 4.9** Provenance mean ring-ring phenotypic correlation coefficients for tracheid length (n=13). Significant correlations in bold, p-values in brackets.

	Ring 2	Ring 4	Ring 6	Ring 8	Ring 10
Ring 2	1	<b>0.76</b> (0.003)	0.35 (0.247)	0.29 (0.332)	0.38 (0.203)
Ring 4		1	<b>0.66</b> (0.015)	<b>0.70</b> (0.008)	<b>0.79</b> (0.001)
Ring 6			1	<b>0.83</b> (0.000)	<b>0.78</b> (0.002)
Ring 8				1	<b>0.82</b> (0.000)
Ring 10					1

Provenance mean phenotypic correlations were high and significant between ring two and ring four, ring four and rings six, eight and 10 and the highest between rings six and eight (Table 4.9). This indicates that provided a suitable number of trees are assessed per provenance, it is possible to obtain a reasonable prediction of tracheid length in subsequent rings by age four. In this study each provenance mean was made up of 81 trees.

Ring-ring additive genetic correlations were also variable and had large standard errors (Table 4.10). No additive genetic correlations could be calculated for ring eight as the family within provenance variance component was zero for this ring.

**Table 4.10** Ring-ring additive genetic correlations for tracheid length.

	Ring 2	Ring 4	Ring 6	Ring 8	Ring 10
Ring 2	1	-0.30 ± 0.59	0.34 ± 0.43	n.e. <sup>1</sup>	0.85 ± 0.15
Ring 4		1	1.10 ± 0.10	n.e.	0.21 ± 0.50
Ring 6			1	n.e.	0.04 ± 0.39
Ring 8				1	n.e.
Ring 10					1

<sup>1</sup> not estimable.

During the period of time in which the wood of the respective rings was being formed, the trees sampled would have been subjected to both random and patterned environmental variation as a result of climatic conditions and of changing competition with other trees in the trial. Nicholls (1967) has speculated that these factors could affect the variance components and hence genetic parameter estimates. Given the low heritabilities discussed in the previous section, it could mean that unpredictable environmental sources of variation play a major role in determining tracheid length in any particular year and that individual trees respond in an unpredictable and random manner that cannot be quantified from these data.

#### 4.3.7.2 Age-age within core correlations

Individual tree and family mean within core age-age phenotypic correlations were also calculated. The correlations among the different ages may reflect their autocorrelation due to their derivation, however, the methodology is no different in principle to that used to determine correlations between growth characters such as height or diameter at breast height at different times in the trees life span.

These estimates were markedly higher than the ring-ring phenotypic correlations (Table 4.11). The correlations indicate that tracheid length determined from an age four core is highly correlated with tracheid length determined from a core removed from an age six or age eight tree, but is less well correlated with mean tracheid length determined on a core from an age ten tree. It is probably not feasible to remove a suitable diameter core (10-12 mm) that would minimize the probability of damaging tracheids, from a tree much younger than four, without killing the tree. Therefore, the age two data has little practical value.

**Table 4.11** Individual tree age-age phenotypic correlation coefficients for tracheid length, above diagonal, and family mean age-age phenotypic correlations (N=109) below diagonal. Significant correlations in bold, p-values in brackets.

	Age2	Age4	Age6	Age8	Age10
Age2	1	<b>0.88</b> (0.000)	<b>0.72</b> (0.000)	<b>0.55</b> (0.000)	<b>0.32</b> (0.000)
Age4	<b>0.88</b> (0.000)	1	<b>0.89</b> (0.000)	<b>0.76</b> (0.000)	<b>0.54</b> (0.000)
Age6	<b>0.71</b> (0.000)	<b>0.90</b> (0.000)	1	<b>0.93</b> (0.000)	<b>0.74</b> (0.000)
Age8	<b>0.60</b> (0.000)	<b>0.80</b> (0.000)	<b>0.95</b> (0.000)	1	<b>0.89</b> (0.000)
Age10	<b>0.57</b> (0.000)	<b>0.75</b> (0.000)	<b>0.88</b> (0.000)	<b>0.95</b> (0.000)	1

The additive genetic correlations between successive ages were all positive and strong, an indication that the same genes are controlling fiber length at all ages considered in this study (Table 4.12). The magnitude of the associated standard errors indicates that they are estimated with a reasonable degree of accuracy. Based on the additive genetic correlations, selection could be carried out at a very young age. Should you want to carry out early selection for tracheid length age four is likely to be the most practical age for early selection. This would be governed by tree size at the time of sampling.

**Table 4.12** Age-age within core additive genetic correlations for tracheid length.

	Age 2	Age 4	Age 6	Age 8	Age 10
Age 2	1	0.85 ± 0.24	0.65 ± 0.34	0.94 ± 0.09	1.21 ± 0.31
Age 4		1	0.81 ± 0.40	0.83 ± 0.35	0.90 ± 0.21
Age 6			1	1.08 ± 0.10	0.87 ± 0.14
Age 8				1	0.72 ± 0.33
Age 10					1

#### 4.3.7.3 Ring - age correlations

Of more interest for practical application are the correlations between individual ring tracheid length and mean age tracheid length. Possibly of most interest is the correlation between ring four, an age at which a small piece of wood representing only the outer most ring could be removed non destructively from a tree, and the mean tracheid length from an age ten tree because it is equivalent to half rotation for pulpwood in South Africa. Removal of only a small piece of wood from the outer growth ring would minimize damage to the tree, simplify sample handling due to its small size, and facilitate rapid maceration with minimal additional sample processing.

The phenotypic correlation between ring four and age ten ( $r = 0.64$ ) is reasonably high, and significant (Table 4.13). Unfortunately the genetic correlation is negative and the standard error is large (Table 4.14). Although many of the ring-age phenotypic correlations are strong and significant (Table 4.14), the additive genetic correlations are disappointing, variable and associated with large standard errors (Table 4.13). This approach therefore does not appear to have any merit.

**Table 4.13** Individual tree ring-age phenotypic correlation coefficients for tracheid length. Significant correlations in bold, p-values in brackets.

	<b>Age4</b>	<b>Age6</b>	<b>Age8</b>	<b>Age10</b>
<b>Ring 4</b>	0.89 (0.000)	0.87 (0.000)	0.79 (0.000)	0.64 (0.000)
<b>Ring 6</b>	0.46 (0.000)	0.81 (0.000)	0.85 (0.000)	0.77 (0.000)
<b>Ring 8</b>	0.14 (0.000)	0.36 (0.000)	0.69 (0.000)	0.77 (0.000)
<b>Ring 10</b>	-0.28 (0.000)	-0.16 (0.000)	0.02 (0.000)	0.48 (0.000)

**Table 4.14** Individual tree ring-age additive genetic correlations for tracheid length.

	<b>Age2</b>	<b>Age4</b>	<b>Age6</b>	<b>Age8</b>	<b>Age10</b>
<b>Ring 4</b>	-0.28 ± 0.45	-0.21 ± 0.76	-0.04 ± 0.55	-0.31 ± 0.60	-0.48 ± 0.47
<b>Ring 6</b>	0.35 ± 0.42	0.54 ± 0.43	0.80 ± 0.15	0.87 ± 0.12	0.52 ± 0.35
<b>Ring 8</b>	n.e. <sup>1</sup>	n.e.	n.e.	n.e.	n.e.
<b>Ring 10</b>	0.84 ± 0.16	0.52 ± 0.50	0.19 ± 0.46	0.15 ± 0.56	0.40 ± 0.45

<sup>1</sup> not estimable.

#### 4.4 Conclusions

Contrary to most reports in the literature, the findings in this study show that tracheid length is under very weak or negligible additive genetic control. Pith-to-bark trends and actual tracheid length are similar to what other authors have reported. Within ring tracheid length distribution was normal, the frequency distribution is what would be expected for a metric trait. Differences between provenances were statistically significant, but the magnitude of these differences is unlikely to be of any practical value. For all rings and ages the difference between the best and worst family did not exceed 0.5 mm. This range of variation would not be usable in an applied breeding program.

Variation in tracheid length appears to be controlled at the individual tree level. If tracheid length is under strong non-additive genetic control, or if epistatic effects are important this variation would need to be captured operationally through cloning desirable individuals. Alternatively the environmental variables may be exerting the most influence on phenotypic variation. This would need to be tested in a clonal trial.

Age-age additive genetic correlations indicate that selection for tracheid length could be carried out as early as two years of age. But given the low level of additive genetic variation, tracheid length should not be included as a selection criteria in *P. patula* breeding programs in South Africa.

## Chapter 5

### Variation and Genetic Control of Tracheid Cross-Sectional Properties

#### 5.1 Importance of tracheid cross-sectional properties

Some authors have concluded that the wood density of *P. taeda* is the most important wood quality trait for pulping, because of its good correlation with pulping properties, and its ease of measurement (Van Buijtenen, 1967; Zobel and Jett, 1995). Similar conclusions have been reached for other pine species such as *P. radiata* (Kibblewhite, 1999), *P. elliottii* (Wangaard *et al.*, 1966) and *P. patula* (Myburgh and Mackenzie, 1966). Wood density is important since it has a strong influence on wood handling, transport costs and overall process throughputs based on the pulp mill mass balance relationship of wood substance in, and kraft pulp or cellulose out (Kibblewhite, 1999). Kibblewhite (1999) rightly points out that wood density is not necessarily a good indicator of the suitability of the raw material for the manufacture of particular paper grades. Rather, it is the chemistry and morphology of tracheids in pine pulp wood that ultimately determine pulp quality and appropriate end use (Kibblewhite, 1999). Relative to the hardwoods, pines have a simple wood structure. The basic element in pine wood is a long narrow conductive fiber or tracheid; approximately 5% or less is composed of other tissues such as rays and resin canals (Burley *et al.* 1972).

Paper is formed from the collapsed and interwoven remnants of these fibrous cells of wood from which it is made. The strength of paper is defined by the physical strength of the fibers, by the degree of physical contact between them, and by the degree of ionic bonding formed between adjacent fiber walls, which have been structurally stripped to their inner layers during processing (Smook, 1992). For a

given pulp, subjected to a standard cooking regime, the degree of inter-wall contact between the fibers will depend to some extent on the propensity of the fibers to collapse in upon themselves under the specific conditions used and, in part, on their length and flexibility (Smook, 1992).

Quality of pine tracheids for pulp is related to the chemical constituents of the tracheid and the three basic dimensions of the tracheid, namely length, diameter and cell wall thickness (Smook, 1992). These characteristics, in turn, govern such tracheid properties as flexibility and strength. The shape of the cells and the proportion of wall material to lumen might be expected to determine the stiffness of the cell and the ease with which it would collapse and become flattened. Very good predictions (80 percent and higher) of the properties of kraft pulp handsheets have been obtained by measurement of the primary tracheid characteristics and their related properties (Dinwoodie 1965, 1966 and Wangaard *et al.* 1966). Frequently, it is not the cell component itself, but rather the ratios, such as cell length to wall thickness, or to lumen size, that are important.

Tracheid diameter and wall thickness are reportedly both closely tied to wood density. Despite having relatively high published heritabilities, they are seldom included in tree breeding programs because of their reported overall influence on the more easily measured wood density (Zobel and Jett, 1995). Tracheid diameter has been shown to be under weaker genetic control than other tracheid characteristics (Zobel and Jett, 1995). Van Buijtenen (1967) points out that smaller tracheid diameters usually improve major strength properties of paper. The diameter of the earlywood tracheids contributes to wood density variation while the effect of the diameter of the latewood tracheids is often negligible (Zobel and van Buijtenen, 1989).

Wall thickness of the cell wall is of prime importance in all wood qualities. Wood with thick cell walls tends to produce paper with a poor printing surface and poor burst strength. Thick walled cells do not bend easily and do not collapse easily upon

refining, this inhibits chemical bonding (Smook, 1992). Although such tracheids do not bond readily, they are resistant to beating and they increase the tearing strength of paper (Dadswell and Wardrop, 1959). Thin-walled tracheids collapse more easily and become ribbon-like, thus providing a large surface area for bonding (Dadswell and Wardrop, 1959). Handsheets made from thin-walled tracheids are much weaker in tearing strength but are superior in other properties. Wall thickness also has a major effect on the bending, tear and tensile strengths of paper. Few studies in the past have been directed solely at wall thickness, most relate to changing the proportion of thick-walled cells, through the control of latewood percentage, or the amount of thin-walled juvenile wood, by changing rotation ages (Zobel and Jett, 1995). More gains may be achievable by manipulating site and rotation age than are possible from traditional tree breeding for additive genetic traits. However, genetic manipulation of the wood properties of the juvenile core of pines grown on short rotations in the tropics and subtropics remains an attractive option.

## **5.2 Genetic control of tracheid cross-sectional properties**

Until recently, tracheid cross-sectional properties have been difficult and expensive to measure. For this reason there have been few comprehensive genetic studies that require large numbers of families, and suitable numbers of individuals from each family to be assessed. Goggans (1964), in one of the earliest studies to determine the heritability of tracheid cross-sectional properties, investigated 19 wood and tracheid characteristics in seven and eight-year-old loblolly pine grown on two sites in the U.S.A. Five trees from six and eight open-pollinated half-sib families were sampled at each site. Although, the heritability estimates were high ( $>0.50$ ), Goggans (1964) did point out that the small number of parents represented in the progeny tests precluded direct use of the numerical heritability values. Nevertheless, the conclusion was drawn that most wood properties were under moderate to strong genetic control.

Evans *et al.* (1995) first reported on an automated wood microstructure analyser for pines, SilviScan®, that was developed for the rapid measurement of tracheid cross-sectional dimensions. SilviScan® directly measures tracheid radial and tangential diameter using image analysis, and wood density profiles by x-ray densitometry (Evans *et al.*, 1995). Mathematical combination of density profiles with the tracheid diameter profiles is used to calculate coarseness, wall thickness, perimeter and specific surface area profiles (see Evans *et al.* (1995) for details).

A number of studies with *P. radiata* have been conducted using this equipment (Nyakuengama *et al.*, 1998, 1999, 2000, and Shelbourne *et al.* 1997). Shelbourne *et al.* (1997) reported that for 13-year-old *P. radiata* grown in New Zealand, individual heritabilities for tracheid cross-sectional dimensions and wood density were high, ranging from 0.53 for tangential diameter to 1.09 for radial diameter. Heritabilities for the derived traits showed intermediate values. That study was based on a sample of eight trees from each of 25 open-pollinated half-sib families. Parents of the 25 families were selected for extreme values of wall thickness, and as a result, heritability estimates are likely to be inflated (Shelbourne *et al.*, 1997). Shelbourne *et al.* (1997) were also able to calculate individual heritabilities by regressing offspring means on parental values. These estimates were more conservative, but heritability estimates were still high ranging from 0.37 for tangential diameter to 0.67 for wood density and radial diameter. The general conclusion that can be drawn from that study, is that tracheid cross-sectional dimensions are under strong additive genetic control.

Nyakuengama *et al.* (1999) conducted a similar study using 25-year-old *P. radiata* grown in Australia. Between nine and 11 trees were sampled from each cross in a 4 by 4 diallel progeny test. Genetic parameter estimates were higher than those reported by Shelbourne *et al.* (1997). Four of the seven individual heritability estimates exceeded one. A value exceeding one reflects genetic sampling error in the estimation of the family variance component. Most estimates were also

associated with large standard errors. Due to the small number of parents used (4), results from this study must be treated with some caution.

Hannrup (1999) has reported that genetic effects were indicated to be strong for earlywood radial and tangential tracheid diameter and weak for cell wall thickness in 33-year-old *Pinus sylvestris* grown in Sweden. Analysis of variance revealed no significant differences ( $p = 0.19$  to  $0.65$ ) between parent trees at any of the ages studied (Hannrup, 1999).

A few studies, discussed above, have been reported in *P. radiata* (Nyakuengama *et al.*, 1999; Shelbourne *et al.*, 1997) and *P. sylvestris* (Hannrup, 1999), and a large study is underway in the south-eastern U.S.A. with *P. taeda*. This study represents the first and most comprehensive evaluation of the tracheid cross-sectional properties of *P. patula*. Nine hundred and ninety eight samples representing genetic material from a diverse geographic background were used. The large sample size provides the opportunity to accurately estimate genetic parameters for tracheid cross-sectional properties.

The procedure used to prepare samples and measure tracheid cross-sectional properties has been outlined in Chapter 2. Five tracheid cross-sectional properties, radial diameter (RD), tangential diameter (TD), lumen diameter (LD), wall area (WA) and cell wall thickness (WT), were measured or calculated from direct measurements using an image analysis system at the CSIR laboratories in Durban, South Africa.

## 5.3 Results and discussion

### 5.3.1 Individual tree phenotypic variation

Simple statistics using area weighted mean core values were calculated for 993 trees (Table 5.1). Five samples were misplaced in the laboratories, therefore no data other than density and tracheid length is available for those samples.

Few reports on the variation of tracheid cross-sectional properties in *P. patula* are available. Wright and Sluis-Cremer (1992) studied tracheid morphology in 13 *P. patula* trees grown in South Africa. The study was restricted to rings four, eight and 12. They reported a mean lumen diameter of 28.30  $\mu\text{m}$ , mean tracheid diameter of 34.10  $\mu\text{m}$  and that mean wall thickness varied from 2.90  $\mu\text{m}$  (earlywood) to 4.90  $\mu\text{m}$  (latewood). In a separate study Wright and Malan (1991) reported that cell wall thickness varied from 5.60  $\mu\text{m}$  to 7.38  $\mu\text{m}$  between trees. Although only five trees were studied, they were the same age as the trees in this study, but grown on a different site. Depending on the age of the trees sampled, other authors report cell wall thickness to vary from 5.00  $\mu\text{m}$  to 6.21  $\mu\text{m}$ , tracheid diameter to vary from 38.30  $\mu\text{m}$  to 53.60  $\mu\text{m}$  and lumen diameters of 43.40  $\mu\text{m}$  to 43.60  $\mu\text{m}$  in *P. patula* (Palmer *et al.* 1984; Palmer and Gibbs, 1974). The mean values and ranges obtained in this study are similar to what other authors have found for *P. patula* (Table 5. 1).

**Table 5.1** Mean, standard deviations (SD), minimum and maximum values for individual tree tracheid cross-sectional properties; radial diameter (RD), tangential diameter (TD), lumen diameter (LD), wall area (WA) and wall thickness (WT).

Variable	n	Mean	SD	Minimum	Maximum
RD ( $\mu\text{m}$ )	993	41.34	3.131	32.68	55.36
TD ( $\mu\text{m}$ )	993	34.85	2.031	28.25	41.57
LD ( $\mu\text{m}$ )	993	26.51	2.299	19.16	34.53
WA ( $\mu\text{m}^2$ )	993	504.92	73.493	315.19	782.98
WT ( $\mu\text{m}$ )	993	5.13	0.652	3.11	7.55

By contrast, the radial and tangential tracheid diameters reported for *P. radiata* are smaller than what has been found in this study. Both studies carried out on *P. radiata* are in good agreement, and report area weighted mean tangential tracheid diameter to be close to 29.00  $\mu\text{m}$  and radial tracheid diameter to be 34.00  $\mu\text{m}$  (Nyakuengama *et al.*, 1999; Shelbourne *et al.*, 1997). Wheeler *et al.* (1966) reported that tracheid tangential diameter in *P. taeda* can range from 34.70  $\mu\text{m}$  to 47.60  $\mu\text{m}$  and that differences between individual trees were significant. *Pinus patula* appears to have tracheid characteristics that are intermediate between *P. radiata* and *P. taeda*. However, direct comparisons are difficult because of the potentially large effect that age and site may have on the results. Different laboratories and measurement techniques also preclude direct comparison.

Large individual tree-to-tree phenotypic variation exists for all five tracheid cross-sectional properties (Table 5.1). In all cases the highest individual tree value (maximum) is close to double the lowest individual tree value (minimum). Provided that the traits are under reasonable levels of additive genetic control, potential for selection and improvement appears promising. For all traits, individual tree, area weighted mean values followed a normal distribution.

To be able to make a comparison with the published reports of Nyakuengama *et al.*, (1999) and Shelbourne *et al.* (1997), tracheid diameter profiles (radial and tangential) and wood density data were used to calculate the same variables as produced by SilviScan® analysis of radial wood strips (Table 5.2).

**Table 5.2** Mean, standard deviations (SD), minimum and maximum values for individual tree SilviScan® derived tracheid cross-sectional properties; coarseness (CS), wall thickness (WTS), specific surface (SS) and perimeter (PM).

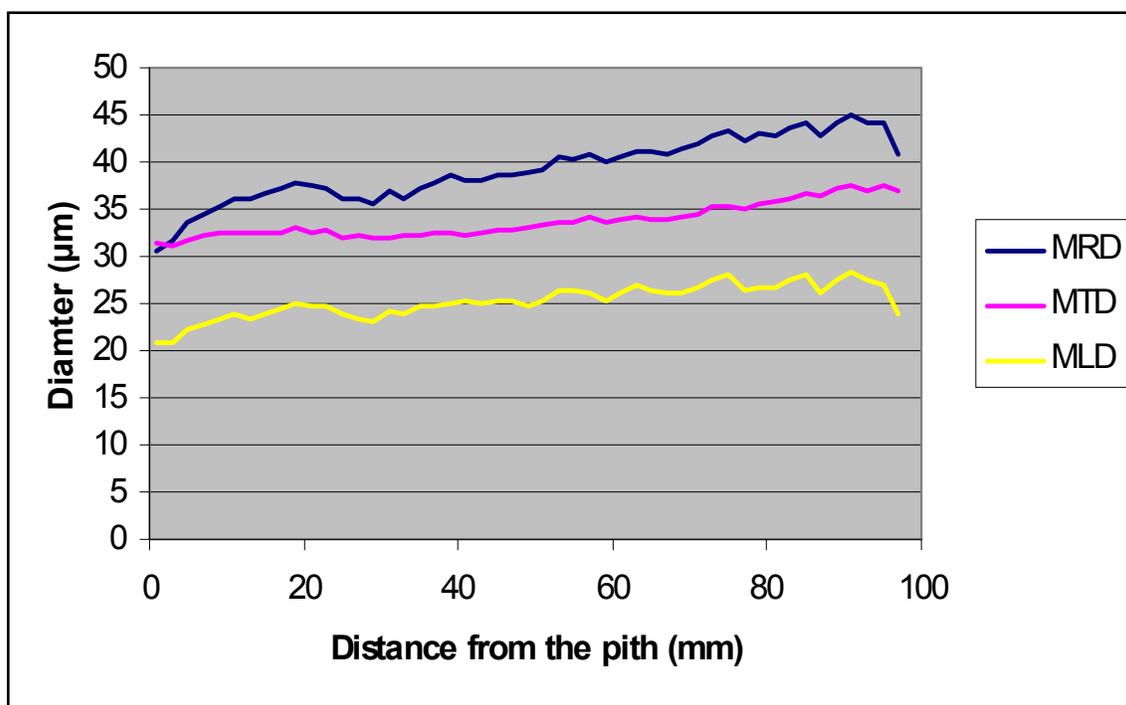
Variable	n	Mean	SD	Minimum	Maximum
CS ( $\mu\text{g m}^{-1}$ )	993	627.65	89.468	385.64	941.31
WTS ( $\mu\text{m}$ )	993	2.74	0.283	1.86	3.70
SS ( $\text{m}^2 \text{kg}^{-1}$ )	993	246.01	25.462	180.30	358.15
PM ( $\mu\text{m}$ ).	993	152.37	9.774	125.32	193.86

Mean coarseness in *P. radiata* has been reported to vary between 440 and 503  $\mu\text{g m}^{-1}$ , mean wall thickness to be 2.70  $\mu\text{m}$ , mean specific surface 280  $\text{m}^2 \text{kg}^{-1}$  and mean perimeter to be in the range 122 to 128  $\mu\text{m}$  (Nyakuengama *et al.*, 1999; Shelbourne *et al.*, 1997). The two studies conducted by Nyakuengama *et al.* (1999) and Shelbourne *et al.* (1997) are in good agreement. *Pinus patula* has higher coarseness, specific surface and perimeter values than *P. radiata* (Table 5.2). The specific surface area should correlate with the surface available for inter-fiber bonding and light scattering in paper, and may be an important trait (Evans *et al.*, 1995).

Of most concern is the large difference between the wall thickness (5.13  $\mu\text{m}$ ) calculated using the image analysis system at the CSIR (Table 5.1), and the wall thickness (2.74  $\mu\text{m}$ ) derived using the SilviScan® method (Table 5.2). As discussed earlier in this section, wall thickness estimates obtained in this study using the CSIR image analysis system are in good agreement with what other authors have reported for *P. patula*. The correlation between these two variables (WT and WTS) was moderate ( $r = 0.46$ ), and statistically significant ( $P < 0.0001$ ). However, it was much lower than one would expect for two approaches designed to measure the same trait. The data presented above strongly suggests that wall thickness determined using SilviScan® is a different trait than wall thickness determined using the CSIR image analysis system.

### 5.3.2 Pith-to-bark trends

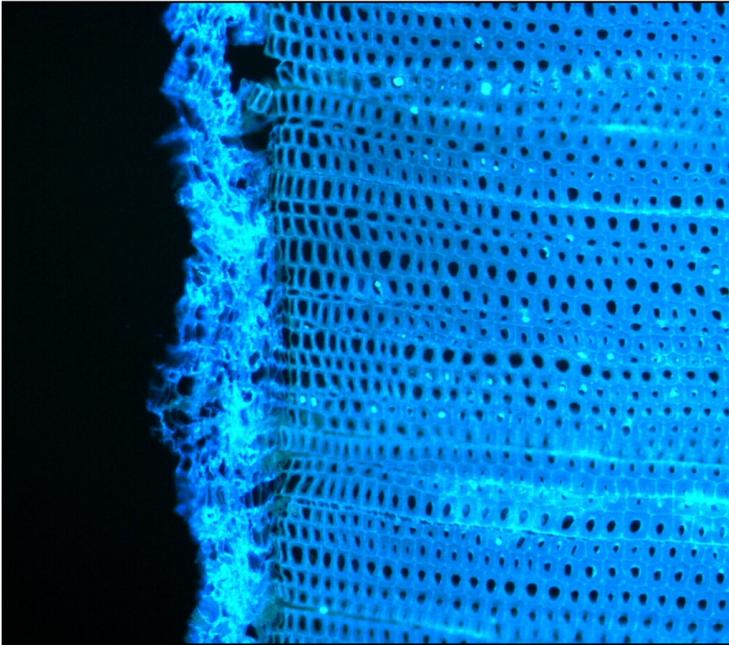
No detailed pith-to-bark trends for tracheid cross-sectional properties have been published for *P. patula*. To obtain some indication of what the general pith-to-bark trends are for these five tracheid properties, data from a subset of seventy-nine trees with the same core radius (97 mm) were pooled and a mean value was calculated for each measurement point (every second mm).



**Figure 5.1** Pith-to-bark trends for mean tracheid diameter properties. Mean radial diameter (MRD), mean tangential diameter (MTD) and mean lumen diameter (MLD). Based on a sub-sample of 79 trees.

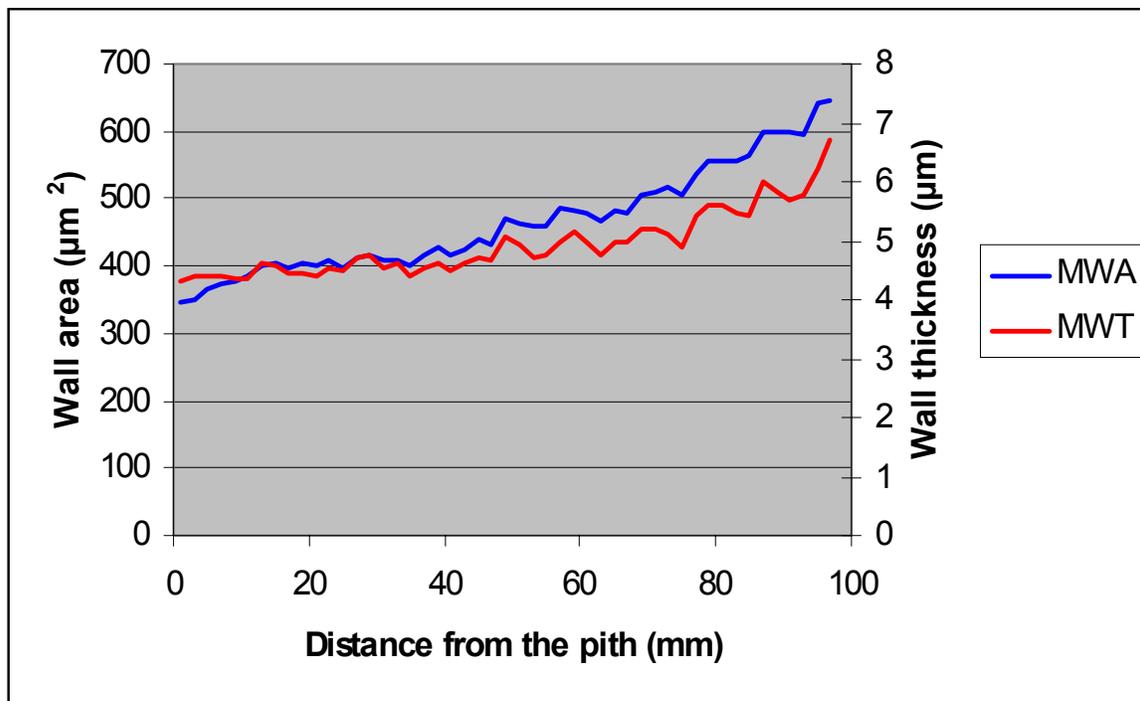
Tracheid diameter (radial and tangential) increases gradually from the pith-to-bark (Figure 5.1). Tracheid radial diameter shows the most variation from pith-to-bark, increasing from 30  $\mu\text{m}$  to 45  $\mu\text{m}$ . The peaks and troughs evident in radial and lumen diameter correspond to latewood and earlywood respectively. Tracheid tangential diameters are less variable and do not change dramatically between earlywood and latewood.

Mean lumen diameter also shows a gradual increase from pith-to-bark (Figure 5.1), but appears to have stabilized during the last three to four years of growth (20 mm). The reduction in tracheid radial diameter and lumen diameter can be accounted for at the last measurement point. The trees in this study were sampled at the end of winter and therefore the last measurement taken closest to the bark would be only latewood (Figure 5.2).



**Figure 5.2** Example of a typical digital image from the section of the core closest to the bark, depicting thick walled latewood before the commencement of spring growth. Sample 105, x10 magnification.

Both wall thickness and wall area are derived in a similar way, and as expected they are highly correlated ( $r = 0.88$ ) and show a similar pith-to-bark trend. Both increase steadily from pith-to-bark and do not appear to be levelling off yet (Figure 5.3). On the contrary, during the past three to four growing seasons (20 mm) there has been a rapid increase in mean tracheid wall thickness and mean wall area. This corresponds with what was reported in Chapter 3, where a dramatic increase in latewood density was evident for the core region represented by growth rings eight, nine and ten (R8-10). The increase in the percentage of latewood in the latter years of growth will also be playing an important role in the observed trend (Figure 5.3). The wood anatomy data confirms that a change has occurred and that the trees are producing a different kind of wood that could be indicative of a change from juvenile to mature wood.



**Figure 5.3** Pith-to-bark trends for mean tracheid properties. Mean wall area (MWA) and mean wall thickness (MWT). Based on a sub-sample of 79 trees.

### 5.3.3 Provenance variation

#### 5.3.3.1 CSIR measured tracheid cross-sectional properties

No reports could be found in the literature on the magnitude of provenance variation for tracheid cross-sectional properties in *P. patula* or other pine species of commercial importance, such as *P. elliottii*, *P. taeda* and *P. radiata*. In that respect, this is a unique study. Results from the analysis of variance have shown that differences between provenances were highly significant ( $P < 0.005$ ) for all five tracheid cross-sectional properties (Appendix 6). Provenance area weighted mean tracheid cross-sectional properties are presented in Table 5.3

**Table 5.3** Provenance area weighted mean tracheid cross-sectional properties; radial diameter (RD), tangential diameter (TD), lumen diameter (LD), wall area (WA) and wall thickness (WT). Ranked on mean tracheid wall thickness (WT).

Provenance	RD ( $\mu\text{m}$ )	R <sup>1</sup>	TD ( $\mu\text{m}$ )	R	LD ( $\mu\text{m}$ )	R	WA ( $\mu\text{m}^2$ )	R	WT ( $\mu\text{m}$ )	R
Corralitla	42.29	6	35.23	6	26.82	6	527.37	2	5.29	1
Ingenio del Rosario	40.95	7	34.89	7	26.08	7	513.00	6	5.28	2
Zacualtipan	40.57	9	34.26	11	25.79	12	496.48	9	5.16	3
El Manzanal	42.40	4	35.90	2	27.52	4	527.81	1	5.15	4
Pinal de Amoles	40.57	8	34.33	10	25.93	9	496.64	8	5.14	5
Tlacotla	39.98	12	34.71	8	25.87	10	493.84	10	5.14	6
Conrado Castillo	38.51	13	32.84	13	24.19	13	467.97	13	5.13	7
Llano de las Carmonas	40.37	10	34.53	9	25.98	8	491.23	11	5.10	8
Potrero de Monroy	40.27	11	34.23	12	25.84	11	487.28	12	5.08	9
Santa Maria Papalo	43.09	2	35.39	4	27.61	3	516.96	4	5.07	10
Ixtlan	42.37	5	35.32	5	27.35	5	512.61	7	5.06	11
SA control	43.07	3	35.54	3	27.76	2	514.66	5	5.05	12
El Tlacuache	44.11	1	36.39	1	28.82	1	525.58	3	4.97	13
Mean	41.43		34.89		26.58		505.49		5.13	
SD	1.580		0.902		1.205		18.122		0.088	
Minimum	38.51		32.84		24.19		467.97		4.97	
Maximum	44.11		36.39		28.82		527.81		5.29	
Range	5.60		3.55		4.63		59.84		0.32	

R<sup>1</sup> Provenance ranking for respective trait.

Provenance ranking was relatively stable for all three tracheid diameter measurements (RD, TD and LD). All four southern provenances, El Tlacuache, Ixtlan, Santa Maria Papalo and El Manzanal had larger diameter tracheids and large lumens. It appears that the wood of *var. longipedunculata* has quite different characteristics to the wood of *var. patula*. The South African control had similar tracheid diameters to these three provenances. Conrado Castillo and Potrero de Monroy all had consistently smaller diameter tracheids, both radial and tangential, and smaller lumen diameters (Table 5.3). Due the smaller size of the tracheids from these two provenances, they also had the lowest mean wall area per tracheid (Table 5.3).

Once again, the four southern most provenances stood out, and had the thinnest cell walls (Table 5.3). The interrelationship between the traits discussed in previous chapters and this chapter is the topic of the following chapter. It is, however, worth noting at this point that despite having the largest tracheids with the thinnest cell walls, that the southern four provenances (*var. longipedunculata*) all had high area weighted mean wood density. Evidence presented so far demonstrates that the wood of *var. patula* and *var. longipedunculata* is markedly different.

### 5.3.3.2 Derived tracheid cross-sectional properties

Using the original data from the CSIR image analysis system, four additional tracheid properties were derived as described in Chapter 2. They were, mean tracheid area (TArea), mean number of tracheids per square millimeter (NoTrach), mean percentage of cell wall per square millimeter (PCell) and Runkel ratio (RR). Differences between provenances were highly significant ( $P < 0.0001$ ) for all four derived tracheid cross-sectional properties (Appendix 6). Provenance area weighted mean tracheid cross-sectional derived properties are presented in Table 5.4.

Kibblewhite (1999) schematically demonstrated that a piece of wood can have the same density and volume but that the number and dimensions of the tracheids can vary. This is likely to affect the suitability of a raw material for the manufacture of particular grades of paper (Kibblewhite, 1999). Variation at the provenance level was investigated for the derived variables.

The northern most provenance Conrado Castillo had the smallest tracheids, and the four provenances El Manzanal, Ixtlan, Santa Maria Papalo, and El Tlacuache, representing *var. longipedunculata* had the largest tracheids (Table 5.4). As a direct result of this, Conrado Castillo had the most tracheids (253) per square millimeter and El Tlacuache the least (201). Similarly, these two provenances had the highest and lowest percentage of cell wall per unit area (Table 5.4). The relationship

between these derived tracheid properties and tracheid length and wood density will be explored in Chapter 6. The differences between these two provenances are large enough to cause differences in paper properties.

**Table 5.4** Provenance area weighted mean derived tracheid properties; mean tracheid area (TArea), mean number of tracheids per square millimetre (NoTrach), mean percentage of cell wall per square millimetre (PCell), and Runkel ratio (RR). Ranked on mean Runkel ratio.

Provenance	TArea ( $\mu\text{m}^2$ )	R <sup>1</sup>	NoTrach (n/mm <sup>2</sup> )	R	PCell (%)	R	Runkel ratio	R
Conrado Castillo	3977.58	13	253.09	1	53.61	1	0.43	1
Ingenio del Rosario	4496.51	7	224.61	7	52.24	2	0.41	2
Zacualtipan	4374.94	10	230.78	4	51.91	3	0.40	3
Tlacotla	4367.51	11	231.04	3	51.61	5	0.40	4
Pinal de Amoles	4385.64	9	230.46	5	51.62	4	0.40	5
Corralitla	4691.47	6	215.55	8	51.50	6	0.40	6
Potrero de Monroy	4337.99	12	232.65	2	51.46	8	0.40	7
Llano de las Carmonas	4389.86	8	230.27	6	51.48	7	0.40	8
El Manzanal	4796.04	4	211.38	11	50.15	9	0.38	9
Ixtlan	4718.55	5	215.54	9	49.84	11	0.37	10
Santa Maria Papalo	4810.88	3	211.78	10	49.90	10	0.37	11
SA control	4823.30	2	210.35	12	49.53	12	0.37	12
El Tlacuache	5063.74	1	201.40	13	48.16	13	0.35	13
Mean	4556.46		222.99		51.00		0.39	
SD	289.709		13.643		1.419		0.021	
Minimum	3977.58		201.40		48.16		0.35	
Maximum	5063.74		253.09		53.61		0.43	
Range	1086.16		51.69		5.45		0.08	

R<sup>1</sup> Provenance ranking for respective trait.

Tracheid characteristics and their effects often cannot be handled as discrete units. Runkel ratio, also known as the double wall thickness ratio, has been reported to account for 58% of the variation in paper properties (Zobel and Jett, 1995). Runkel (1952), cited by Dinwoodie (1966), indicated that the suitability of a species for pulpwood depended on whether the ratio was less than unity. If the ratio is less than one, such material is considered best because tracheids will collapse, become

ribbon-like and provide a large area for inter-fibre bonding. When the ratio is greater than one, tracheids tend to be stiff, resistant to beating and tend to retain their rounded shape during sheet formation with little area available for inter-fibre bonding (Dinwoodie, 1966). For all provenances and the local seed orchard control, the Runkel ratio (RR) was less than one (Table 5.5).

**Table 5.5** Provenance mean Runkel ratio with Waller-Duncan k-ratio multiple range t-test grouping (P=0.05). Means with the same letter are not significantly different.

Provenance	Variety	RR	Waller Duncan
Conrado Castillo	<i>patula</i>	0.440	A
Ingenio del Rosario	<i>patula</i>	0.418	B
Zacualtipan	<i>patula</i>	0.417	B
Tlacotla	<i>patula</i>	0.414	B
Corralitla	<i>patula</i>	0.414	B
Llano de las Carmonas	<i>patula</i>	0.411	B
Potrero de Monroy	<i>patula</i>	0.410	B
Pinal de Amoles	<i>patula</i>	0.406	B
Ixtlan	<i>longipedunculata</i>	0.387	C
El Manzanal	<i>longipedunculata</i>	0.382	C
Santa Maria Papalo	<i>longipedunculata</i>	0.381	C
El Tlacuache	<i>longipedunculata</i>	0.354	D

In earlier chapters of this thesis, it has been shown that Conrado Castillo could be an outlier provenance. Using Runkel ratio, a statistically significant (P=0.05) separation of the material into four groups was possible. The four groups were, Conrado Castillo, var. *patula*, var. *longipedunculata* and El Tlacuache (Table 5.5), emphasizing again the distinct difference between the wood properties of the two varieties of *P. patula*. If Runkel ratio does account for a large percentage of the variation in paper properties this is an extremely important finding that needs to be confirmed by pulping trees from the two varieties of *P. patula*.

### 5.3.3.3 SilviScan® derived tracheid cross-sectional properties

Differences between provenances were highly significant ( $P < 0.0001$ ) for all four SilviScan® derived tracheid cross-sectional properties (Appendix 6).

**Table 5.6** Provenance area weighted mean SilviScan® derived tracheid properties; coarseness (CS), wall thickness (WTS), specific surface (SS) and perimeter (PM). Ranked on mean tracheid perimeter.

Provenance	CS ( $\mu\text{g m}^{-1}$ )	R <sup>1</sup>	WTS ( $\mu\text{m}$ )	R	SS ( $\text{m}^2 \text{kg}^{-1}$ )	R	PM ( $\mu\text{m}$ )	R
El Tlacuache	716.4	1	2.96	1	227.9	13	161.0	1
SA Control	655.7	4	2.78	5	241.5	9	157.2	2
Santa Maria Papalo	651.4	5	2.76	6	244.1	8	157.0	3
El Manzanal	679.6	2	2.89	2	232.6	12	156.6	4
Ixtlan	657.7	3	2.81	3	239.7	11	155.4	5
Corralitla	625.3	7	2.68	9	251.2	4	155.0	6
Ingenio del Rosario	633.5	6	2.78	4	241.4	10	151.7	7
Llano de las Carmonas	604.2	9	2.69	8	250.8	5	149.8	8
Pinal de Amoles	589.9	11	2.62	13	257.2	1	149.8	9
Zacualtipan	607.6	8	2.70	7	249.6	7	149.7	10
Tlacotla	601.5	10	2.68	10	250.4	6	149.4	11
Potrero de Monroy	586.1	12	2.62	12	256.1	2	149.0	12
Conrado Castillo	569.4	13	2.66	11	253.1	3	142.7	13
Mean	629.1		2.74		245.8		152.6	
SD	41.85		0.102		8.91		4.89	
Minimum	569.4		2.62		227.9		142.7	
Maximum	716.4		2.96		257.2		161.0	
Range	147.0		0.34		29.3		18.3	

R<sup>1</sup> Provenance ranking for respective trait.

The southern provenances, var. *longipedunculata*, had higher coarseness values and the difference between El Tlacuache and Conrado Castillo was large and significant (Table 5.6). Based on these values, these two provenances are likely to produce paper with distinctly different properties. Provenance differences were also large for specific surface and cell perimeter (Table 5.6).

### 5.3.4 Family variation

#### 5.3.4.1 CSIR measured tracheid cross-sectional properties

Differences between families within provenances were statistically significant ( $p > 0.001$ ) for tracheid radial, tangential and lumen diameter. Differences between families were also significant for mean tracheid wall area but were not significant for mean tracheid cell wall thickness (Appendix 6). The result for cell wall thickness is similar to the one reported for mean tracheid length in Chapter 2 and is contrary to what has been reported by other authors (Zobel and Jett, 1995). This will have implications for the genetic parameter estimates.

For all traits, phenotypic variation, at similar levels to that for growth traits, exists between the best and worst families, varying from 17% for tracheid wall thickness to 34% for lumen diameter (Table 5.7). Only two (families 26 and 295) of the ten bottom ranking families for wall thickness are from var. *patula* (Table 5.7). Differences between the best and worst families were also large for the derived traits, varying from 53% for mean tracheid area and mean number of tracheids per square millimeter to 20% for percentage cell wall (Table 5.8). These large differences between the best and worst families provide an early indication that selection for these traits is likely to lead to substantial gain. In the previous section, large, significant differences between provenances were evident. This is reinforced in this section with large differences evident between families.

**Table 5.7** Family mean area weighted tracheid cross-sectional properties; radial diameter (RD), tangential diameter (TD), lumen diameter (LD), wall area (WA) and wall thickness (WT). Top 10 (above the dotted line) and bottom 10 families ranked on wall thickness.

Family	Provenance	RD ( $\mu\text{m}$ )	R <sup>1</sup>	TD ( $\mu\text{m}$ )	R	LD ( $\mu\text{m}$ )	R	WA ( $\mu\text{m}^2$ )	R	WT ( $\mu\text{m}$ )	R
66	Corralitla	42.74	21	36.05	14	26.89	37	556.75	9	5.53	1
38	Ingenio del Rosario	40.94	62	34.87	49	25.64	83	532.01	17	5.49	2
8	Potrero de Monroy	43.02	18	35.16	40	26.73	40	546.83	11	5.48	3
225	Conrado Castillo	38.93	100	32.92	105	23.71	108	496.75	68	5.47	4
289	Tlacotla	41.10	58	35.59	26	26.07	65	533.36	14	5.46	5
53	Ingenio del Rosario	40.29	75	34.95	45	25.60	85	528.77	19	5.45	6
257	Zacualtipan	40.59	70	35.67	23	26.04	66	527.85	20	5.43	7
57	Corralitla	43.15	16	35.62	25	27.02	32	546.53	12	5.42	8
160	Santa Maria Papalo	45.09	8	35.70	21	27.70	21	563.36	7	5.40	9
63	Corralitla	41.04	59	34.63	60	25.71	77	522.62	27	5.40	10
170	Santa Maria Papalo	44.66	10	36.20	12	29.24	8	512.52	42	4.86	99
295	Tlacotla	39.51	92	34.45	68	26.20	60	466.34	98	4.86	100
128	El Tlacuache	44.54	11	36.63	9	29.28	6	515.90	34	4.85	101
80	El Manzanal	41.39	48	35.98	15	27.89	17	498.10	66	4.85	102
119	El Tlacuache	43.94	12	36.69	8	29.26	7	515.93	33	4.82	103
121	El Tlacuache	41.92	36	35.12	43	27.71	20	484.49	79	4.79	104
168	Santa Maria Papalo	41.61	43	34.58	63	27.24	27	477.69	89	4.78	105
153	Ixtlan	45.01	9	35.45	29	29.00	10	499.88	63	4.77	106
26	Potrero de Monroy	38.33	103	34.05	88	25.74	75	448.46	108	4.76	107
107	El Tlacuache	40.86	64	34.58	64	26.79	39	463.00	103	4.72	108
	Mean	41.93		35.24		26.97		511.86		5.13	
	SD	2.02		0.91		1.48		32.12		0.33	
	Minimum	36.71		31.52		22.56		442.10		4.72	
	Maximum	46.68		37.87		30.25		571.79		5.53	
	Range	9.98		6.35		7.68		129.69		0.82	

R<sup>1</sup> - Rank out of 108 for respective trait

#### 5.3.4.2 Derived tracheid cross-sectional properties

For the derived tracheid properties (Table 5.8), only families from var. *longipedunculata* are ranked amongst the bottom ten families for Runkel ratio, while

five of the top ten families for Runkel ratio are from Conrado Castillo. Family-within-provenance effects are consistent and strong. No other published data are available for *P. patula* to compare ranges and the magnitude of variation at the family level for tracheid cross-sectional properties.

**Table 5.8** Family mean area weighted derived tracheid cross-sectional properties; mean tracheid area (TArea), mean number of tracheids per square millimeter (NoTrach), mean percentage of cell wall per square millimeter (PCell), and Runkel ratio (RR). Top 10 (above the dotted line) and bottom 10 families ranked on wall thickness.

Family	Provenance	TArea ( $\mu\text{m}^2$ )	R <sup>1</sup>	NoTrach (n/mm <sup>2</sup> )	R	PCell (%)	R	RR	R
225	Conrado Castillo	4030.70	102	250.06	7	56.14	1	0.47	1
238	Conrado Castillo	3638.40	108	276.45	1	55.91	2	0.46	2
305	Tlacotla	4150.06	97	242.22	13	54.13	3	0.44	3
243	Conrado Castillo	4112.90	99	244.01	11	54.07	4	0.44	4
38	Ingenio del Rosario	4492.05	55	224.50	53	53.73	5	0.43	5
53	Ingenio del Rosario	4434.54	67	227.67	42	53.31	11	0.43	6
241	Conrado Castillo	3838.57	107	261.64	2	53.29	13	0.42	7
227	Conrado Castillo	3982.80	104	251.75	6	53.45	7	0.42	8
63	Corralitla	4476.33	60	226.12	48	53.27	14	0.42	9
289	Tlacotla	4601.41	40	218.69	70	53.45	8	0.42	10
102	El Manzanal	5414.46	3	186.62	106	48.74	96	0.35	99
141	Ixtlan	4794.57	21	210.10	89	48.20	99	0.35	100
80	El Manzanal	4688.20	28	215.47	82	47.65	102	0.35	101
124	El Tlacuache	5550.06	1	180.82	108	48.00	100	0.35	102
130	El Tlacuache	5199.51	7	193.95	102	47.26	104	0.34	103
123	El Tlacuache	5392.54	4	188.96	105	47.16	106	0.34	104
128	El Tlacuache	5131.18	8	196.07	101	47.46	103	0.34	105
170	Santa Maria Papalo	5089.98	9	198.33	100	47.11	107	0.34	106
153	Ixtlan	5019.83	13	200.75	97	47.23	105	0.33	107
119	El Tlacuache	5076.58	11	199.22	99	46.72	108	0.33	108
	Mean	4534.54		224.03		51.13		0.39	
	SD	363.16		17.16		1.87		0.03	
	Minimum	3638.40		180.82		46.72		0.33	
	Maximum	5550.06		276.45		56.14		0.47	
	Range	1911.66		95.62		9.42		0.14	

R<sup>1</sup> - Rank out of 108 for respective trait

#### 5.3.4.3 SilviScan® derived tracheid cross-sectional properties

Some published information is available on tracheid cross-sectional properties in *P. radiata* (Nyakuengama *et al.*, 1999; Shelbourne *et al.*, 1997). Shelbourne *et al.* (1997) provide family mean values for tracheid properties determined using SilviScan® from rings 6 to 13 for twenty-five open-pollinated *P. radiata* families. Although fewer families were used, the difference between the best and worst families were 18%, 18%, 16% and 11% for coarseness, wall thickness, specific surface and perimeter respectively. Differences between the best and worst families were much larger in this study, ranging from 23% for cell perimeter to 41% for coarseness (Table 5.9). If it can be shown that specific surface area correlates with the surface available for inter-fiber bonding and light scattering in paper as reported by Evans *et al.* (1995), this could be an important trait in a breeding program. The existence of usable variation (26%) between families has been shown in this study (Table 5.9).

Once again, the families from Conrado Castillo and var. *longipedunculata* dominate the top and bottom families, seven of the ten bottom families for perimeter area are from Conrado Castillo (Table 5.9).

**Table 5.9** Family mean area weighted SilviScan® derived tracheid cross-sectional properties; coarseness (CS), wall thickness (WTS), specific surface (SS) and perimeter (PM). Ranked on mean tracheid perimeter. Top 10 (above the dotted line) and bottom 10 families ranked on wall thickness.

Family	Provenance	CS ( $\mu\text{g m}^{-1}$ )	R <sup>1</sup>	WTS ( $\mu\text{m}$ )	R	SS ( $\text{m}^2 \text{kg}^{-1}$ )	R	PM ( $\mu\text{m}$ )	R
124	El Tlacuache	803.56	1	3.17	1	212.58	108	168.99	1
163	Santa Maria Papalo	735.45	8	2.91	12	229.99	98	168.45	2
102	El Manzanal	736.40	7	2.94	11	229.38	99	166.64	3
123	El Tlacuache	758.07	3	3.04	5	220.63	105	166.18	4
148	Ixtlan	753.89	4	3.03	6	221.87	104	165.50	5
131	El Tlacuache	766.73	2	3.11	3	215.44	107	164.30	6
130	El Tlacuache	710.05	12	2.89	13	232.55	96	163.50	7
128	El Tlacuache	747.72	5	3.08	4	218.02	106	162.35	8
170	Santa Maria Papalo	684.12	16	2.82	27	238.09	85	161.72	9
160	Santa Maria Papalo	718.76	10	2.95	10	228.33	100	161.59	10
243	Conrado Castillo	582.37	87	2.68	69	250.22	46	145.12	99
26	Potrero de Monroy	555.73	104	2.56	102	262.67	9	144.75	100
301	Tlacotla	576.90	93	2.66	73	253.53	32	144.12	101
225	Conrado Castillo	594.41	80	2.76	45	243.62	65	143.69	102
212	Pinal de Amoles	544.99	108	2.54	106	264.93	3	142.95	103
227	Conrado Castillo	582.06	88	2.72	54	246.10	57	142.84	104
233	Conrado Castillo	548.86	107	2.58	95	260.38	14	141.48	105
228	Conrado Castillo	565.36	100	2.67	72	252.93	35	141.37	106
241	Conrado Castillo	553.35	105	2.62	84	256.98	25	140.33	107
238	Conrado Castillo	550.32	106	2.69	66	250.62	45	136.44	108
	Mean	625.60		2.73		246.40		152.15	
	SD	50.98		0.14		12.10		5.93	
	Minimum	544.99		2.52		213.73		136.44	
	Maximum	766.73		3.15		268.38		168.45	
	Range	221.73		0.62		54.66		32.01	

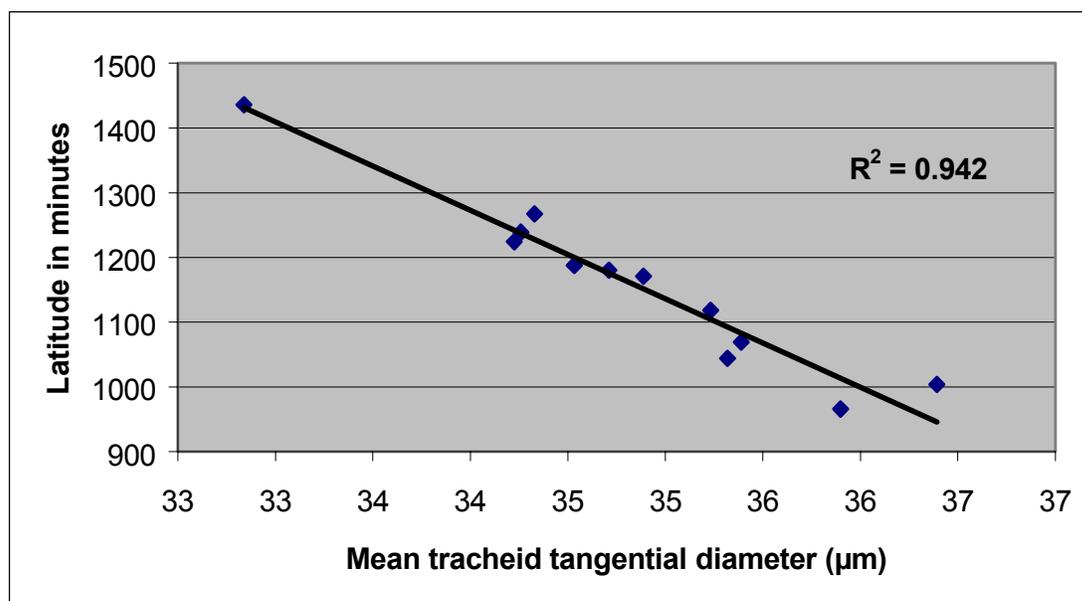
R<sup>1</sup> Rank out of 108 for respective trait

### 5.3.5 Correlation with collection sites

In the preceding chapters, the existence of a clinal pattern for density traits and tracheid length has been demonstrated. This was also investigated for the tracheid cross-sectional properties. Provenance mean values for tracheid cross-sectional properties were correlated with collection site climatic data as outlined in the materials and methods. For all tracheid cross-sectional traits of interest, other than tracheid wall thickness, correlations with the latitude of the provenance were strong and significant. This demonstrates that a strong clinal trend exists for tracheid cross-sectional properties in *P. patula* (Table 5.10). The correlation between tangential diameter and latitude of provenance approached one ( $r = 0.97$ ), and is the strongest reported in this thesis (Figure 5.4).

**Table 5.10** Correlation of provenance weighted mean tracheid cross-sectional properties with collection site latitude, longitude, mean annual precipitation (MAP) and mean annual temperature (MAT). Significant correlations in bold, p-values in brackets.

Variable	Lat. (N)	Long. (W)	MAP (mm)	MAT (°C)
RD	<b>-0.90</b> (0.000)	<b>-0.77</b> (0.003)	0.44 (0.156)	0.33 (0.300)
TD	<b>-0.97</b> (0.000)	<b>-0.81</b> (0.002)	0.36 (0.257)	0.22 (0.492)
LD	<b>-0.94</b> (0.000)	<b>-0.77</b> (0.004)	0.34 (0.278)	0.31 (0.319)
WA	<b>-0.90</b> (0.000)	<b>-0.81</b> (0.002)	0.54 (0.073)	0.25 (0.434)
WT	0.24 (0.452)	0.06 (0.850)	0.33 (0.295)	-0.24 (0.453)
TArea	<b>-0.94</b> (0.000)	<b>-0.79</b> (0.002)	0.41 (0.192)	0.29 (0.357)
NoTrach	<b>0.95</b> (0.000)	<b>0.81</b> (0.002)	-0.42 (0.172)	-0.28 (0.385)
PCell	<b>0.88</b> (0.000)	<b>0.67</b> (0.018)	-0.20 (0.530)	-0.35 (0.270)
RR	<b>0.86</b> (0.000)	<b>0.67</b> (0.018)	-0.19 (0.548)	-0.34 (0.285)



**Figure 5.4** Mean provenance tracheid tangential diameter plotted against provenance latitude, demonstrating a strong north to south increase (clinal trend) in mean tracheid tangential diameter.

Correlations with the provenance longitude were also statistically significant although they were weaker. None of the correlations with the climatic parameters, mean annual precipitation and mean annual temperature were significant.

### 5.3.6 Genetic parameters

Individual heritability estimates for the tracheid cross-sectional properties varied from negligible for tracheid wall thickness ( $h^2 = 0.02$ ), percentage cell wall ( $h^2 = 0.04$ ) and Runkel ratio ( $h^2 = 0.02$ ), to moderately strong for tracheid radial diameter ( $h^2 = 0.52$ ) (Table 5.11 and Table 5.12). Estimates for most of the tracheid cross-sectional properties were generally of a similar magnitude to the estimates for density traits (Chapter 3). The standard errors of the heritability estimates were all low ( $<0.10$ ), an indication that the estimates are reliable. The low estimate for tracheid wall thickness

was unexpected, as it has been reported that cell wall thickness is under moderate to high levels of additive genetic control (Zobel and Jett, 1995; Nyakuengama *et al.*, 1999; Shelbourne *et al.*, 1997).

The individual heritabilities for tracheid radial and tangential diameter estimated in this study are about half the magnitude of reported individual heritabilities for the same traits in *P. radiata* (Shelbourne *et al.*, 1997). Standard errors, however, are much smaller in this study. Co-efficients of variation vary from 5% to 13% (Table 5.11 and Table 5.12), these are similar to those found in *P. radiata* where the co-efficient of variation was less than 10% for all wood properties (Nyakuengama *et al.*, 1999). Typical co-efficients of variation for growth traits in *P. patula* tend to be much higher than this, and have been reported to range from 11.5% for height to 33.2% for diameter growth and 37.7% for tree volume at eight years of age (Barnes *et al.*, 1992).

**Table 5.11** Variance component and parameter estimates for area weighted mean tracheid cross-sectional properties; radial diameter (RD), tangential diameter (TD), lumen diameter (LD), wall area (WA) and wall thickness (WT).

	RD	TD	LD	WA	WT
Mean	41.330	34.850	26.510	504.920	5.129
Variance Component					
Prov	2.24	0.78	1.35	207.73	0.000000
Fam(Prov)	1.27	0.27	0.41	240.34	0.001462
Error	6.12	2.77	3.17	3318.70	0.253510
Parameters					
$\sigma^2_{\text{phen}}$	7.39	3.04	3.58	3559.04	0.254972
$\sigma^2_A$	3.81	0.81	1.24	721.01	0.004386
$h^2_b$	0.52±0.10	0.27±0.08	0.35±0.09	0.20±0.07	0.02±0.05
$h^2_{f(b)}$	0.65	0.47	0.54	0.39	0.05
CV	0.07	0.05	0.07	0.12	0.10
GCV	0.05	0.03	0.04	0.05	0.01
$P^2_b$	0.30	0.26	0.38	0.06	0.00

For this population the GCV ranged from 1% for mean cell wall thickness to 7% for mean tracheid area and mean number of tracheids per square millimetre (Table 5.11 and 5.12). Sufficient genetic variation exists for successful selection for most tracheid cross-sectional properties. Provenance variance expressed as a percentage of the total phenotypic variance ( $P^2_b$ ), was zero for tracheid wall thickness but varied from 0.06 to 0.38 for other tracheid cross-sectional traits. For most traits that have been considered, the estimates indicate that provenance effects are strong and that they should be taken into account in a breeding program.

**Table 5.12** Variance component and parameter estimates for area weighted mean derived tracheid cross-sectional properties; mean tracheid area (TArea), mean number of tracheids per square millimetre (NoTrach), mean percentage of cell wall per square millimetre (PCell), and Runkel ratio (RR).

	TArea	NoTrach	PCell	Runkel ratio
Mean	4534.00	224.06	51.12	0.39
Variance Component				
Prov	77749.80	172.23	1.36	0.000333
Fam(Prov)	36638.70	78.49	0.20	0.000019
Error	209002.10	509.29	14.88	0.002761
Parameters				
$\sigma^2_{phen}$	245640.80	587.78	15.08	0.002780
$\sigma^2_A$	109916.10	235.48	0.61	0.000058
$h^2_b$	0.45±0.10	0.40±0.09	0.04±0.06	0.02±0.05
$h^2_{f(b)}$	0.61	0.58	0.11	0.06
CV	0.11	0.11	0.08	0.13
GCV	0.07	0.07	0.02	0.02
$P^2_b$	0.32	0.29	0.09	0.12

Due to a lack of published information for comparative purposes, radial and tangential tracheid diameters were used to calculate the same variables estimated by SilviScan®. This provided some data for comparison. Genetic parameters were calculated for the SilviScan® derived traits (Table 5.13). These parameter estimates were compared with those reported for *P. radiata*.

The heritability estimates for the SilviScan® derived traits for *P. patula* ranged from 0.30 to 0.45, an indication that all traits are under moderate to strong additive genetic control. These estimates were approximately half the size of the estimates reported by Shelbourne *et al.* (1997) for open-pollinated half-sib *P. radiata* families, but were similar in magnitude to the estimates derived by Shelbourne *et al.* (1990) using parent-offspring regression co-efficients to estimate heritabilities. Shelbourne *et al.* (1997) reported individual heritability estimates of 0.49, 0.28, 0.29 and 0.26 for coarseness (CS), wall thickness (WTS), specific surface (SS) and perimeter (PM) respectively.

**Table 5.13** Variance component and parameter estimates for area weighted mean SilviScan® derived tracheid cross-sectional properties; coarseness (CS), wall thickness (WTS), specific surface (SS) and perimeter (PM).

	CS	WTS	SS	PM
Mean	626.84	2.74	246.16	152.25
Variance Component				
Prov	1672.90	0.0098	72.94	22.09
Fam(Prov)	796.97	0.0056	43.19	10.48
Error	4621.00	0.0479	392.29	59.66
Parameters				
$\sigma^2_{\text{phen}}$	5417.97	0.0535	435.48	70.13
$\sigma^2_A$	2390.90	0.0168	129.58	31.44
$h^2_b$	0.44±0.10	0.31±0.08	0.30±0.08	0.45±0.10
$h^2_{f(b)}$	0.61	0.51	0.50	0.61
CV	0.12	0.08	0.08	0.06
GCV	0.08	0.05	0.05	0.04
$P^2_b$	0.31	0.18	0.17	0.32

The GCV estimates ranged from four to 9% and the provenance variance expressed as a percentage of the total phenotypic variance ( $P^2_b$ ) from 0.17 to 0.32. For the derived traits provenance effects remain strong and important from a practical

perspective, and sufficient genetic variation exists for exploitation in a breeding program.

### **5.3.7 Phenotypic and additive genetic correlations**

Phenotypic correlations were calculated on individual tree values and family means. Phenotypic correlations between the tracheid cross-sectional properties radial, tangential and lumen diameter were strong and positive (Table 5.14). Tracheid wall area was also strongly positively correlated with tracheid radial and tangential diameter but weakly correlated with lumen diameter. Tracheid radial diameter, tangential diameter and lumen diameter were weakly correlated with tracheid cell wall thickness, but wall area was strongly and positively correlated with cell wall thickness (Table 5.14).

Due the nature of their derivation, mean tracheid area and the number of tracheids per square millimeter were highly negatively correlated (Table 5.15). Runkel ratio and mean percentage of cell wall per square millimeter (PCell) were also highly correlated, This can be explained by the large influence of cell wall thickness in the derivation of both these traits. It is probably not necessary to calculate both these variables as heritability estimates were also of a similar magnitude.

Phenotypic correlations among the SilviScan® derived variables were compared with those published for *P. radiata* (Nyakuengama *et al.*, 1999; Shelbourne *et al.*, 1997). Phenotypic correlations for all traits were in the same direction, but the estimates in this study were all slightly higher than those published for *P. radiata* by Shelbourne *et al.* (1997). The estimates published by Nyakuengama *et al.* (1999) were closer to the ones in this study (Table 5.16).

**Table 5.14** Phenotypic correlations between area weighted mean tracheid cross-sectional properties; radial diameter (RD), tangential diameter (TD), lumen diameter (LD), wall area (WA) and wall thickness (WT). Individual tree above diagonal (n=968) and family mean below diagonal (n=109). Significant correlations in bold, p-values in brackets.

	RD	TD	LD	WA	WT
RD	1	<b>0.78</b> (0.000)	<b>0.80</b> (0.000)	<b>0.64</b> (0.000)	<b>0.24</b> (0.000)
TD	<b>0.89</b> (0.000)	1	<b>0.71</b> (0.000)	<b>0.72</b> (0.000)	<b>0.37</b> (0.000)
LD	<b>0.94</b> (0.000)	<b>0.92</b> (0.000)	1	<b>0.19</b> (0.000)	<b>-0.29</b> (0.000)
WA	<b>0.83</b> (0.000)	<b>0.84</b> (0.000)	<b>0.69</b>	1	<b>0.88</b> (0.000)
WT	0.12 (0.231)	0.15 (0.120)	-0.14 (0.134)	<b>0.61</b> (0.000)	1

**Table 5.15** Phenotypic correlations between area weighted mean derived tracheid cross-sectional properties; mean tracheid area (TArea), mean number of tracheids per square millimeter (NoTrach), mean percentage of cell wall per square millimeter (PCell), and Runkel ratio (RR). Individual tree above diagonal (n=968) and family mean below diagonal (n=109). Significant correlations in bold, p-values in brackets.

	TArea	NoTrach	PCell	RR
TArea	1	<b>-0.98</b> (0.000)	<b>-0.13</b> (0.000)	<b>-0.17</b> (0.000)
NoTrach	<b>-0.99</b> (0.000)	1	<b>0.12</b> (0.000)	<b>0.17</b> (0.000)
PCell	<b>-0.62</b> (0.000)	<b>0.61</b> (0.000)	1	<b>0.98</b> (0.000)
RR	<b>-0.67</b> (0.000)	<b>0.66</b> (0.000)	<b>0.98</b> (0.000)	1

The correlations among the traits derived from the measured radial and tangential tracheid diameters generally reflect their auto-correlation due to their derivation. Phenotypic correlations among all SilviScan® derived traits were statistically

significant and were very strong when calculated on a family mean basis (Table 5.16)

**Table 5.16** Phenotypic correlations between area weighted mean SilviScan® derived tracheid cross-sectional properties; coarseness (CS), wall thickness (WTS), specific surface (SS) and perimeter (PM). Individual tree above diagonal (n=968) and family mean below diagonal (n=109). Significant correlations in bold, p-values in brackets.

	RD	TD	CS	WTS	SS	PM
RD	1	<b>0.78</b> (0.000)	<b>0.70</b> (0.000)	<b>0.36</b> (0.000)	<b>-0.36</b> (0.000)	<b>0.97</b> (0.000)
TD	<b>0.89</b> (0.000)	1	<b>0.72</b> (0.000)	<b>0.43</b> (0.000)	<b>-0.43</b> (0.000)	<b>0.92</b> (0.000)
CS	<b>0.86</b> (0.000)	<b>0.86</b> (0.000)	1	<b>0.91</b> (0.000)	<b>-0.90</b> (0.000)	<b>0.75</b> (0.000)
WTS	<b>0.63</b> (0.000)	<b>0.65</b> (0.000)	<b>0.93</b> (0.000)	1	<b>-0.99</b> (0.000)	<b>0.41</b> (0.000)
SS	<b>-0.62</b> (0.000)	<b>-0.64</b> (0.000)	<b>-0.92</b> (0.000)	<b>-1.00</b> (0.000)	1	<b>-0.41</b> (0.000)
PM	<b>0.99</b> (0.000)	<b>0.95</b> (0.000)	<b>0.89</b> (0.000)	<b>0.66</b> (0.000)	<b>-0.65</b> (0.000)	1

Additive genetic correlations among area weighted tracheid cross-sectional properties were all very strong and positive, standard errors were generally small (Table 5.17). Measurements of tracheid size, radial diameter (RD), tangential diameter (TD), and lumen diameter were all strongly correlated an indication that they are controlled by the same genes.

**Table 5.17** Additive genetic correlations with their standard errors, between area weighted mean tracheid cross-sectional properties.

	RD	TD	LD	WA	WT
RD	1	0.92 ± 0.03	0.96 ± 0.01	1.00 ± 0.00	1.31 ± 0.35
TD		1	1.00 ± 0.00	0.94 ± 0.03	0.99 ± 0.01
LD			1	0.97 ± 0.05	1.16 ± 0.20
WA				1	1.20 ± 0.29
WT					1

Tracheid radial, tangential and lumen diameter was also highly correlated with cell wall area and cell wall thickness (Table 5.17). Additive genetic correlations were larger than the phenotypic correlations. Additive genetic correlations among the derived traits were also generally strong with the percentage of cell wall per square millimeter (PCell) less strongly correlated with mean tracheid area (TArea) and mean number of tracheids per square millimeter (NoTrach) (Table 5.18). Additive genetic correlations were once again larger than the phenotypic correlations.

**Table 5.18** Additive genetic correlations with their standard errors, between area weighted mean derived tracheid cross-sectional properties.

	TArea	NoTrach	PCell	RR
TArea	1	-0.99 ± 0.00	-0.66 ± 0.23	-1.25 ± 0.30
NoTrach		1	0.68 ± 0.22	1.30 ± 0.37
PCell			1	1.05 ± 0.14
RR				1

The additive genetic correlations between cell wall thickness (WTS) and specific surface (SS) and coarseness (CS) and perimeter (PM) were very similar in magnitude to estimates published for *P. radiata* (Nyakuengama *et al.*, 1999; Shelbourne *et al.*, 1997) (Table 5.19). The other additive genetic correlations were in the same direction but much stronger in this study (Table 5.19). Standard errors for all estimates were small.

**Table 5.19** Additive genetic correlations with their standard errors, between weighted mean SilviScan® derived tracheid cross-sectional properties.

	CS	WTS	SS	PM
CS	1	0.92 ± 0.03	-0.92 ± 0.03	0.87 ± 0.04
WTS		1	-1.00 ± 0.00	0.61 ± 0.11
SS			1	-0.60 ± 0.11
PM				1

## 5.4 Conclusions

In this study it has been shown that large individual tree-to-tree phenotypic variation exists for all tracheid cross-sectional properties assessed. Differences between provenances were statistically significant and it has been demonstrated that these differences are strong and important. The four southern most provenances (var. *longipedunculata*) and the most northern provenance Conrado Castillo have different tracheid dimensions than var. *patula*. Based on the differences that have been demonstrated, it is likely that the different varieties of *P. patula* would produce paper with markedly different properties. Testing will be initiated to confirm this.

The presence of a clinal pattern persisted and was the strongest between tracheid tangential diameter and latitude of collection site ( $r = 0.97$ ). Based on the strong correlations between wood properties and provenance latitude, it should be possible to predict what sort of properties can be expected from the other eleven identified provenances of *P. patula* that are not included in this study. The robustness of this can easily be confirmed with a small field study.

Heritability estimates for tracheid dimensions indicate that they are under moderate to strong genetic control with tracheid radial diameter having the highest heritability estimate ( $h^2 = 0.52$ ), reported in this thesis. Standard errors for all heritability estimates were low, demonstrating that the estimates are reasonably accurate and reliable.

To determine tracheid wall thickness the CSIR image analysis system first identifies cell lumen and measures its area assuming a circular shape. Lumen diameter is derived from this measurement. It then identifies boundaries between cells (middle lamella), and calculates cell area within it (including lumen) and diameter. Cell wall thickness is then calculated as the difference between tracheid diameter and lumen diameter, divided by two to get single cell wall thickness. SilviScan® does not

measure cell wall thickness directly either but a different method of derivation is used (Evans *et al.*, 1995). The absolute estimates of cell wall thickness were quite different, with the cell wall thickness derived using the SilviScan® method being approximately half that of the cell wall thickness from the CSIR image analysis system. The heritability estimates also differed dramatically (0.02 vs. 0.31) and the phenotypic correlation between them, although statistically significant, was only moderate ( $r = 0.46$ ). Depending on what method is used to estimate cell wall thickness, different conclusions would be drawn as to what extent this trait is under genetic control and the expected response to selection. Hannrup (1999) has reported that genetic effects were indicated to be weak for cell wall thickness in *Pinus sylvestris*. This is in agreement with what has been found in this study using the data generated from the CSIR image analysis system.

Additive genetic correlations among the CSIR measured tracheid cross-sectional properties were strong and positive. Based on the results presented, selection for any one tracheid trait will lead to a correlated response in the same direction in the other traits. The correlations between the derived traits should be interpreted with some caution due to bias from auto-correlation (the magnitude of which varies, depending on how the variables are derived). Correlations among the wood properties presented in this chapter and growth, wood density and tracheid length traits will be discussed in the next chapter.

## Chapter 6

### Phenotypic and Additive Genetic Correlations Between Growth, Wood Density, Tracheid Length and Tracheid Cross-sectional Properties

#### 6.1 Growth parameters

After wood sampling had been completed, the diameter at breast height and total tree height were assessed on each tree. Mean tree volume was calculated. It is not the intention to report on the growth parameters in any detail, however, the growth data will be used in the following sections of this chapter to examine the nature and magnitude of the correlations between growth traits and wood property traits. The genetic parameters for growth traits are therefore presented in Table 6.1.

**Table 6.1** Variance component and parameter estimates for growth traits, diameter at breast height (DBH), height (HT) and mean tree volume (VOL).

	Dbh	Ht	Vol
Mean	25.04	17.47	0.33
Variance Component			
Prov	0.228020	0.186410	0.000000
Fam(Prov)	0.331770	0.051100	0.000185
Error	8.283440	3.348600	0.008945
Parameters			
$\sigma^2_{\text{phen(prov)}}$	8.615210	3.399700	0.009130
$\sigma^2_A$	0.995310	0.153300	0.000555
$h^2_b$	0.12	0.05	0.06
$h^2_{f(b)}$	0.26	0.12	0.16
CV	0.12	0.11	0.29
GCV	0.04	0.02	0.07
$P^2_b$	0.03	0.05	0.00

Trees for this study were selected on the basis of their size or individual tree volume. For this reason the heritability estimates are likely to be biased and are therefore much lower than the estimates calculated using the complete trial data set at age eight. A heritability of 0.20 has been reported for tree volume for *P. patula* in South Africa (Dvorak et al., 2000), compared to a heritability estimate of 0.06 for the sample of 998 trees used in this study (Table 6.1).

## 6.2 Phenotypic correlations

The association between two characters that can be directly observed is known as a phenotypic correlation. The presence of a phenotypic correlation "per se" does not guarantee a breeder that a causal genetic correlation exists between two traits. In a selection context, phenotypic correlations are therefore less informative as they have no direct genetic interpretation and may be caused by a common environmental factor. The objective of establishing that a phenotypic correlation exists between two characters might be to see if it is feasible to predict the value of one character of a pair, given the value of the other. This could be of importance when, for example, one of the characters is difficult or more expensive to measure but the other is quite easy and cheap to measure. A good example in wood property research is wood density, which is relatively cheap and easy to measure.

Most wood properties have until recently, been difficult, time consuming and costly to measure. Due to these high costs and technical limitations, very few studies have measured the complete range of wood properties. Rather, researchers have been forced to focus on only one or two wood properties at a time. For this reason the correlations between wood properties have generally not been well determined (Zobel and Jett, 1995). In this study a number of traits (discussed in Chapters 3-5) were measured on the same pith-to-bark sample. This provided an ideal opportunity to calculate phenotypic correlations among density, tracheid length and tracheid cross-sectional traits. These have been reported on in this thesis in the preceding

chapters. In this chapter, correlations between traits will be presented and discussed.

### 6.2.1 Phenotypic correlations between growth and wood property traits.

From a tree breeding perspective, the relationship between growth rate and wood properties is extremely important. At some time every tree breeder has asked the question, "If I increase growth rate, what am I doing to the wood properties?". In recent times, with more focus on wood properties in tree breeding programs, this has become an even more critical question. Most phenotypic correlations between wood properties and growth traits, diameter at breast height (DBH), height (HT) and individual tree volume (VOL), were either not statistically significant, or significant and very weak (Table 6.2).

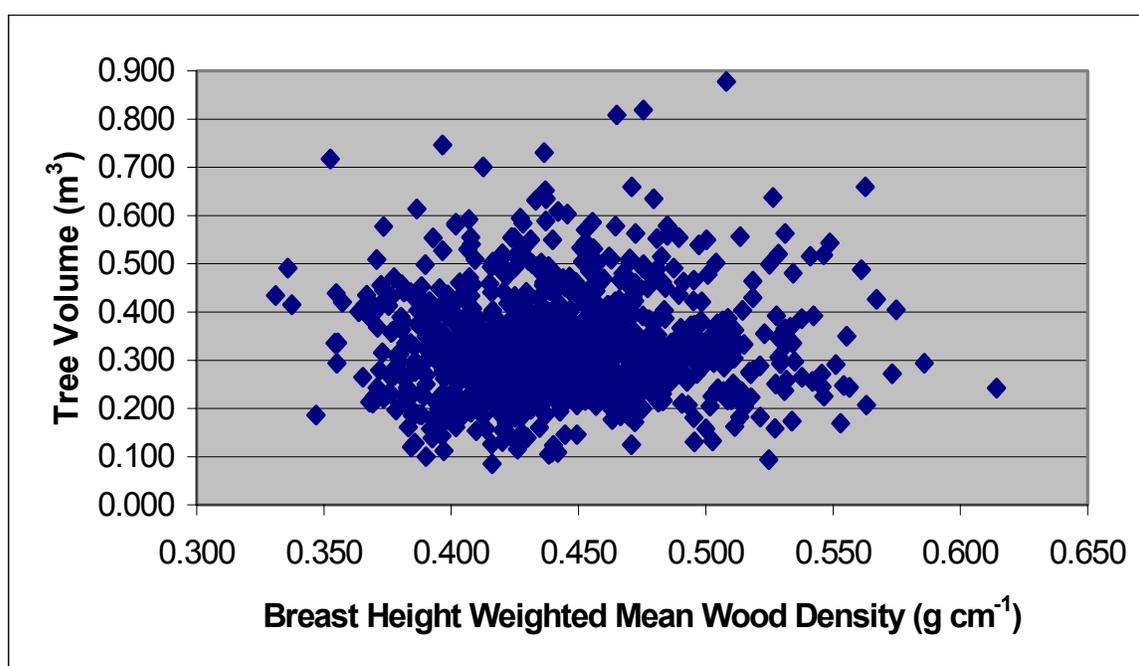
**Table 6.2** Phenotypic correlations between growth and wood density traits. Individual tree on the left (n=972) and family mean on the right (n=109). Significant correlations in bold, p-values in brackets.

	Individual Tree			Family Mean		
	DBH	HT	VOL	DBH	HT	VOL
<b>WMD</b>	-0.01 (0.700)	<b>0.10</b> (0.002)	0.05 (0.148)	-0.18 (0.057)	0.02 (0.864)	<b>-0.21</b> (0.025)
<b>MEWD</b>	0.03 (0.300)	-0.03 (0.390)	0.02 (0.616)	0.13 (0.165)	<b>-0.41</b> (0.000)	<b>-0.20</b> (0.039)
<b>MLWD</b>	<b>-0.09</b> (0.006)	<b>0.18</b> (0.000)	0.02 (0.482)	<b>-0.31</b> (0.001)	<b>0.54</b> (0.000)	0.10 (0.298)
<b>PLW</b>	0.03 (0.345)	<b>0.11</b> (0.000)	<b>0.09</b> (0.007)	0.02 (0.856)	-0.11 (0.242)	-0.15 (0.126)

Zobel and Jett (1995) quote a number of studies where authors have reported a positive correlation between wood properties and height growth. In this study, individual tree and family mean phenotypic correlations between height growth and wood density, in particular mean latewood density, were positive and significant (Table 6.2). Although the individual tree correlation coefficients are statistically

significant, they are not large, but they do indicate that taller trees tend to have higher density latewood. Nyakuengama (1998) has reported weak and statistically non-significant correlations between height and wood density ( $r = 0.08$ ), and tree diameter and wood density ( $r = 0.03$ ) in *P. radiata*. These estimates are similar to those found in this study (Table 6.2).

The family mean correlation coefficient between height growth and mean latewood density was 0.54 (Table 6.2). Fortunately, these correlations are positive. A visual demonstration of the independence of wood density and individual tree volume is presented in Figure 6.1.



**Figure 6.1** Plot of breast height weighted mean wood density against individual tree volume demonstrating the independence of these two traits.

The significant negative family mean phenotypic correlation between mean latewood density and diameter growth can be explained by the provenance performance for these two traits. Based on the sub-sample of trees used in this study, the four provenances that had the highest latewood density (Tlacotla, Zacualtipan, Potrero de Monroy and Ingenio del Rosario), had the lowest mean diameter.

Phenotypic correlations (individual tree and family mean) between tracheid length properties and growth traits were mostly weak and were not statistically significant (Table 6.3). The individual tree correlations between height growth and tracheid length at breast height, although positive and weak, were statistically significant and constant across ages and rings (Table 6.3). Family mean phenotypic correlations were weak and negative between diameter growth and tracheid length traits, while the correlations with height growth were positive. It is possible therefore, to have big trees that have both short and long tracheids.

**Table 6.3** Phenotypic correlations between growth and tracheid length traits. Individual tree on the left (n=968) and family mean on the right (n=109). Significant correlations in bold, p-values in brackets.

	Individual Tree			Family Mean		
	DBH	HT	VOL	DBH	HT	VOL
<b>Ring 4</b>	0.02 (0.501)	<b>0.09</b> (0.004)	<b>0.07</b> (0.038)	-0.05 (0.634)	0.07 (0.474)	0.06 (0.553)
<b>Ring 6</b>	-0.04 (0.216)	<b>0.08</b> (0.011)	0.01 (0.824)	-0.12 (0.198)	0.16 (0.095)	0.05 (0.639)
<b>Ring 8</b>	-0.04 (0.201)	<b>0.07</b> (0.040)	0.00 (0.987)	-0.16 (0.092)	0.19 (0.052)	-0.03 (0.743)
<b>Ring 10</b>	-0.02 (0.449)	<b>-0.08</b> (0.008)	<b>-0.08</b> (0.014)	-0.06 (0.503)	0.14 (0.139)	0.01 (0.950)
<b>MAge4</b>	0.02 (0.621)	<b>0.08</b> (0.012)	0.06 (0.063)	-0.10 (0.307)	-0.05 (0.588)	-0.04 (0.667)
<b>MAge6</b>	-0.03 (0.452)	<b>0.09</b> (0.007)	0.03 (0.347)	-0.16 (0.099)	0.04 (0.649)	-0.03 (0.791)
<b>MAge8</b>	-0.05 (0.178)	<b>0.10</b> (0.004)	0.02 (0.535)	<b>-0.21</b> (0.031)	0.11 (0.254)	-0.05 (0.630)
<b>MAge10</b>	-0.06 (0.087)	<b>0.06</b> (0.069)	-0.01 (0.742)	<b>-0.19</b> (0.044)	0.14 (0.161)	-0.04 (0.687)

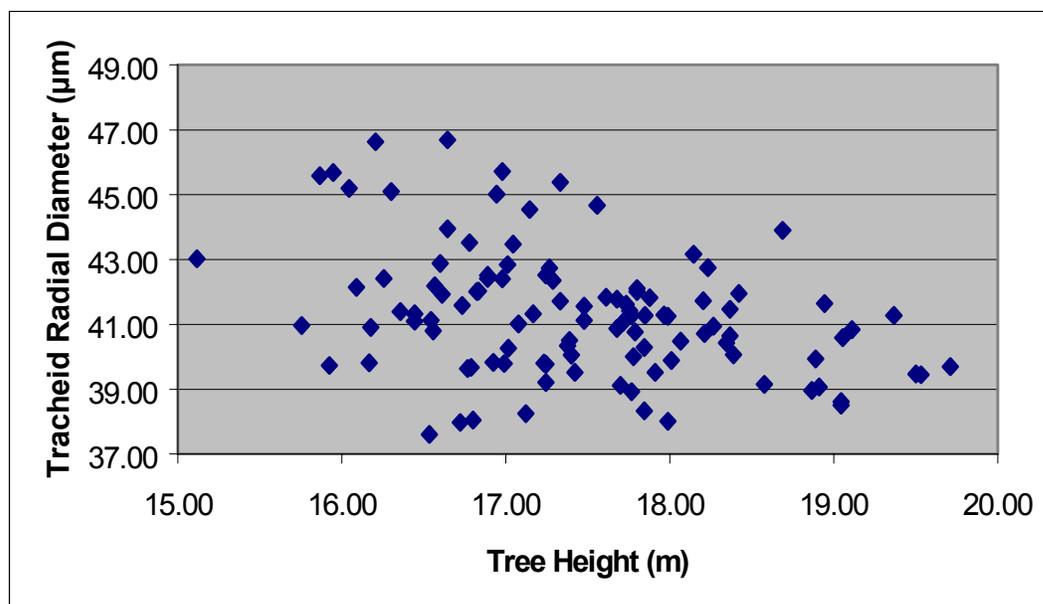
Moderate phenotypic correlations have been reported between growth parameters (HT and DBH) and tracheid radial and tangential diameters in *P. radiata*. These ranged from 0.28 to 0.47 and were statistically significant (Nyakuengama, 1998). Estimates obtained in this study between growth traits and tracheid radial and tangential diameters were much lower ranging from -0.07 to 0.15 (Table 6.4). Phenotypic correlation estimates based on family means were however of a similar

magnitude to those reported by Nyakuengama (1998). At the family mean level, all correlations between height and tracheid cross-sectional properties, except the correlation between height and cell wall area, were significant and relatively strong. Taller families tended to have smaller diameter tracheids in both the radial and tangential plane (Table 6.4 and Figure 6.2). None of the correlations with individual tree volume were significant.

**Table 6.4** Phenotypic correlations between growth and tracheid cross-sectional properties. Individual tree on the left (n=968) and family mean on the right (n=109). Significant correlations in bold, p-values in brackets.

	Individual Tree			Family Mean		
	DBH	HT	VOL	DBH	HT	VOL
<b>RD</b>	<b>0.15</b> (0.000)	<b>-0.07</b> (0.027)	0.06 (0.056)	<b>0.25</b> (0.008)	<b>-0.34</b> (0.000)	0.07 (0.479)
<b>TD</b>	<b>0.08</b> (0.011)	-0.05 (0.104)	0.03 (0.373)	<b>0.16</b> (0.091)	<b>-0.27</b> (0.005)	0.00 (0.999)
<b>LD</b>	<b>0.15</b> (0.000)	<b>-0.09</b> (0.007)	0.05 (0.144)	<b>0.30</b> (0.002)	<b>-0.34</b> (0.000)	0.04 (0.646)
<b>WT</b>	-0.03 (0.367)	0.01 (0.813)	-0.01 (0.700)	0.03 (0.762)	<b>-0.24</b> (0.012)	0.01 (0.897)
<b>WA</b>	0.04 (0.197)	-0.03 (0.283)	0.01 (0.732)	<b>-0.29</b> (0.002)	0.08 (0.424)	-0.02 (0.869)
<b>TArea</b>	<b>0.13</b> (0.000)	<b>-0.07</b> (0.026)	0.05 (0.149)	<b>0.23</b> (0.019)	<b>-0.33</b> (0.001)	0.04 (0.687)
<b>NoTrach</b>	<b>-0.13</b> (0.000)	0.05 (0.102)	-0.06 (0.079)	<b>-0.21</b> (0.027)	<b>0.30</b> (0.002)	-0.05 (0.587)
<b>PCell</b>	<b>-0.08</b> (0.011)	0.06 (0.068)	-0.02 (0.612)	-0.36 (0.000)	<b>0.29</b> (0.003)	-0.04 (0.682)
<b>RR</b>	<b>-0.09</b> (0.003)	0.05 (0.113)	-0.03 (0.289)	<b>-0.39</b> (0.000)	<b>0.31</b> (0.001)	-0.06 (0.532)
<b>CS</b>	<b>0.12</b> (0.000)	-0.03 (0.387)	<b>0.07</b> (0.039)	0.15 (0.124)	<b>-0.31</b> (0.001)	-0.06 (0.539)
<b>SS</b>	<b>-0.08</b> (0.011)	-0.02 (0.616)	-0.06 (0.057)	0.06 (0.534)	<b>-0.25</b> (0.009)	-0.13 (0.193)
<b>WTS</b>	<b>0.08</b> (0.012)	0.02 (0.525)	<b>0.06</b> (0.045)	-0.03 (0.762)	<b>0.24</b> (0.012)	0.14 (0.162)
<b>PM</b>	<b>0.14</b> (0.000)	<b>-0.09</b> (0.007)	0.05 (0.142)	<b>0.23</b> (0.019)	<b>-0.32</b> (0.001)	0.05 (0.644)

Although significant, individual tree correlations between diameter growth and tracheid cross-sectional properties were weak (Table 6.4).



**Figure 6.2** Plot of tree height against family mean tracheid radial diameter demonstrating a moderate trend for taller trees to have smaller diameter tracheids ( $r = -0.34$ ).

### 6.2.2 Phenotypic correlations between wood density and tracheid length traits.

There appears to be a weak to moderate negative phenotypic correlation between tracheid length on a ring basis and weighted mean density and mean earlywood density. Individuals with higher density earlywood appear to have shorter tracheids (Table 6.5). At the family mean level only two of the correlations with ring eight mean tracheid length were statistically significant (Table 6.5). For practical purposes, tracheid length appears to be independent of all wood density traits evaluated in this study.

**Table 6.5** Individual tree phenotypic correlations between tracheid length and wood density traits. Individual tree on the left (n=972) and family mean on the right (n=109). Significant correlations in bold, p-values in brackets.

	Individual Tree				Family Mean			
	Ring 4	Ring 6	Ring 8	Ring 10	Ring 4	Ring 6	Ring 8	Ring 10
<b>WMD</b>	0.12 (0.000)	0.03 (0.428)	<b>-0.15</b> (0.000)	<b>-0.37</b> (0.000)	-0.06 (0.563)	-0.11 (0.279)	-0.18 (0.063)	-0.08 (0.419)
<b>MEWD</b>	0.00 (0.984)	-0.05 (0.131)	<b>-0.17</b> (0.000)	<b>-0.28</b> (0.000)	-0.10 (0.316)	-0.16 (0.099)	<b>-0.23</b> (0.018)	-0.11 (0.245)
<b>MLWD</b>	<b>0.15</b> (0.000)	<b>0.11</b> (0.001)	0.04 (0.167)	<b>-0.08</b> (0.014)	0.07 (0.449)	0.13 (0.172)	0.16 (0.093)	0.08 (0.387)
<b>PLW</b>	0.06 (0.054)	-0.03 (0.354)	<b>-0.16</b> (0.000)	<b>-0.32</b> (0.000)	-0.09 (0.342)	-0.16 (0.109)	<b>-0.19</b> (0.045)	-0.12 (0.209)
	<b>MAge4</b>	<b>MAge6</b>	<b>MAge8</b>	<b>MAge10</b>	<b>MAge4</b>	<b>MAge6</b>	<b>MAge8</b>	<b>MAge10</b>
<b>WMD</b>	<b>0.22</b> (0.000)	<b>0.16</b> (0.000)	<b>0.07</b> (0.033)	<b>-0.08</b> (0.012)	0.07 (0.478)	-0.01 (0.951)	-0.05 (0.580)	-0.08 (0.436)
<b>MEWD</b>	<b>0.09</b> (0.007)	0.04 (0.283)	-0.04 (0.294)	<b>-0.14</b> (0.000)	0.09 (0.346)	-0.02 (0.822)	-0.10 (0.297)	-0.13 (0.175)
<b>MLWD</b>	<b>0.12</b> (0.000)	<b>0.14</b> (0.000)	<b>0.13</b> (0.000)	0.07 (0.037)	-0.08 (0.418)	0.02 (0.832)	0.09 (0.363)	0.11 (0.242)
<b>PLW</b>	<b>0.16</b> (0.000)	<b>0.10</b> (0.005)	0.02 (0.642)	<b>-0.11</b> (0.001)	0.04 (0.706)	-0.04 (0.691)	-0.08 (0.392)	-0.11 (0.246)

### 6.2.3 Phenotypic correlations between wood density and tracheid cross-sectional traits.

All individual tree phenotypic correlations between wood density and tracheid diameter traits (RD, TD and LD), were negative and significant (Table 6.6). At the family mean level mean earlywood density was positively correlated with tracheid diameter traits while correlations with mean latewood density were strong and negative.

Shelbourne et al. (1997) also report negative phenotypic correlations between weighted mean wood density and radial and tangential tracheid diameter, but their estimates were larger, -0.38 and -0.42, respectively. Goggans (19674) reported much lower phenotypic correlations between whole core specific gravity and tracheid

diameter. The estimates ranged from -0.04 to -0.12 and varied between summerwood and springwood (Goggans, 1964).

**Table 6.6** Phenotypic correlations between wood density and tracheid cross-sectional properties. Individual tree on the left (n=968) and family mean on the right (n=109). Significant correlations in bold, p-values in brackets.

	Individual Tree				Family Mean			
	WMD	MEWD	MLWD	PLW	WMD	MEWD	MLWD	PLW
<b>RD</b>	<b>-0.26</b> (0.000)	<b>-0.12</b> (0.000)	<b>-0.17</b> (0.000)	<b>-0.24</b> (0.000)	<b>-0.24</b> (0.012)	<b>0.32</b> (0.001)	<b>-0.59</b> (0.000)	-0.03 (0.795)
<b>TD</b>	<b>-0.14</b> (0.000)	-0.06 (0.084)	<b>-0.16</b> (0.000)	<b>-0.12</b> (0.000)	<b>-0.18</b> (0.057)	<b>0.31</b> (0.001)	<b>-0.57</b> (0.000)	0.04 (0.645)
<b>LD</b>	<b>-0.45</b> (0.000)	<b>-0.25</b> (0.000)	<b>-0.27</b> (0.000)	<b>-0.38</b> (0.000)	<b>-0.29</b> (0.003)	<b>0.32</b> (0.001)	<b>-0.64</b> (0.000)	-0.05 (0.622)
<b>WA</b>	<b>0.11</b> (0.001)	<b>0.11</b> (0.001)	0.00 (0.960)	<b>0.07</b> (0.035)	-0.07 (0.461)	<b>0.28</b> (0.003)	<b>-0.43</b> (0.000)	0.11 (0.270)
<b>WT</b>	<b>0.31</b> (0.000)	<b>0.20</b> (0.000)	<b>0.15</b> (0.000)	<b>0.23</b> (0.000)	0.17 (0.073)	-0.03 (0.725)	0.17 (0.076)	0.14 (0.135)
<b>TArea</b>	<b>-0.22</b> (0.000)	<b>-0.09</b> (0.004)	<b>-0.19</b> (0.000)	<b>-0.20</b> (0.000)	<b>-0.22</b> (0.025)	<b>0.33</b> (0.000)	<b>-0.61</b> (0.000)	0.01 (0.899)
<b>NoTrach</b>	<b>0.21</b> (0.000)	<b>0.11</b> (0.001)	<b>0.15</b> (0.000)	<b>0.21</b> (0.000)	<b>0.25</b> (0.009)	<b>-0.29</b> (0.003)	<b>0.57</b> (0.000)	0.03 (0.786)
<b>PCell</b>	<b>0.46</b> (0.000)	<b>0.28</b> (0.000)	<b>0.21</b> (0.000)	<b>0.37</b> (0.000)	<b>0.35</b> (0.000)	<b>-0.22</b> (0.024)	<b>0.55</b> (0.000)	0.15 (0.115)
<b>RR</b>	<b>0.47</b> (0.000)	<b>0.25</b> (0.000)	<b>0.29</b> (0.000)	<b>0.36</b> (0.000)	<b>0.33</b> (0.001)	<b>-0.24</b> (0.012)	<b>0.58</b> (0.000)	0.14 (0.163)
<b>CS</b>	<b>0.44</b> (0.000)	<b>0.49</b> (0.000)	<b>-0.16</b> (0.000)	<b>0.39</b> (0.000)	<b>0.23</b> (0.016)	<b>0.64</b> (0.000)	<b>-0.65</b> (0.000)	<b>0.41</b> (0.000)
<b>SS</b>	<b>-0.74</b> (0.000)	<b>-0.70</b> (0.000)	0.05 (0.144)	<b>-0.63</b> (0.000)	<b>-0.57</b> (0.000)	<b>-0.77</b> (0.000)	<b>0.57</b> (0.000)	<b>-0.65</b> (0.000)
<b>WTS</b>	<b>0.75</b> (0.000)	<b>0.70</b> (0.000)	<b>-0.06</b> (0.049)	<b>0.66</b> (0.000)	<b>0.55</b> (0.000)	<b>0.77</b> (0.000)	<b>-0.59</b> (0.000)	<b>0.66</b> (0.000)
<b>PM</b>	<b>-0.22</b> (0.000)	-0.05 (0.133)	<b>-0.23</b> (0.000)	<b>-0.18</b> (0.000)	<b>-0.23</b> (0.019)	<b>0.32</b> (0.001)	<b>-0.60</b> (0.000)	0.00 (0.999)

Wood density traits were positively correlated with cell wall thickness, cell wall area and the derived traits, number of tracheids per square millimetre, mean percentage of cell wall per tracheid and Runkel ratio (Table 6.6). This indicates that trees with

higher wood density tend to have more tracheids per square millimetre and thicker walls.

At the family mean level, phenotypic correlations between mean latewood density and CSIR measured traits were mostly strong and negative. However, the phenotypic correlations between cell wall thickness and wood density traits were not significant at the family level (Table 6.6). This is likely to have implications for the genetic correlations.

The phenotypic correlations between SilviScan® derived traits and weighted mean wood density were of a similar magnitude and the same direction as those reported by Shelbourne et al. (1997). The correlation between the SilviScan® derived cell wall thickness and weighted mean wood density is 0.75; and in good agreement with what has been reported for *P. radiata* ( $r = 0.79$ ) by Shelbourne *et al.* (1997).

#### **6.2.4 Phenotypic correlations between tracheid length and cross-sectional traits.**

At the individual tree level, tracheid length was consistently positively correlated with tracheid diameter traits (RD, TD and LD). These correlations were positive but weak and consistent across rings and ages (Table 6.7). Correlations between mean tracheid area and number of tracheids per square millimetre are similar in magnitude but opposite in direction, as expected. Most correlations with SilviScan® derived traits were significant at the 0.05 level.

**Table 6.7** Individual tree phenotypic correlations between tracheid length and tracheid cross-sectional properties (n=968). Significant correlations in bold, p-values in brackets.

	Ring 4	Ring 6	Ring 8	Ring 10	MAge4	MAge6	MAge8	MAge10
<b>RD</b>	<b>0.13</b> (0.000)	<b>0.13</b> (0.000)	<b>0.08</b> (0.012)	<b>0.13</b> (0.000)	<b>0.08</b> (0.012)	<b>0.11</b> (0.001)	<b>0.11</b> (0.001)	<b>0.15</b> (0.000)
<b>TD</b>	<b>0.17</b> (0.000)	<b>0.16</b> (0.000)	<b>0.08</b> (0.015)	0.04 (0.255)	<b>0.14</b> (0.000)	<b>0.18</b> (0.000)	<b>0.17</b> (0.000)	<b>0.16</b> (0.000)
<b>LD</b>	<b>0.12</b> (0.000)	<b>0.13</b> (0.000)	<b>0.15</b> (0.000)	<b>0.25</b> (0.000)	0.05 (0.180)	<b>0.09</b> (0.008)	<b>0.12</b> (0.000)	<b>0.21</b> (0.000)
<b>WA</b>	<b>0.09</b> (0.003)	<b>0.11</b> (0.000)	-0.01 (0.776)	<b>-0.08</b> (0.016)	<b>0.10</b> (0.003)	<b>0.13</b> (0.000)	<b>0.09</b> (0.005)	0.05 (0.173)
<b>WT</b>	0.04 (0.192)	0.06 (0.079)	<b>-0.08</b> (0.015)	<b>-0.19</b> (0.000)	<b>0.09</b> (0.011)	<b>0.09</b> (0.005)	0.04 (0.206)	-0.05 (0.144)
<b>TArea</b>	<b>0.15</b> (0.000)	<b>0.15</b> (0.000)	<b>0.08</b> (0.008)	<b>0.10</b> (0.002)	<b>0.11</b> (0.001)	<b>0.15</b> (0.000)	<b>0.14</b> (0.000)	<b>0.17</b> (0.000)
<b>NoTrach</b>	<b>-0.17</b> (0.000)	<b>-0.15</b> (0.000)	<b>-0.08</b> (0.013)	<b>-0.07</b> (0.027)	<b>-0.13</b> (0.000)	<b>-0.16</b> (0.000)	<b>-0.15</b> (0.000)	<b>-0.16</b> (0.000)
<b>PCell</b>	-0.01 (0.703)	-0.03 (0.292)	<b>-0.15</b> (0.000)	<b>-0.29</b> (0.000)	0.06 (0.087)	0.03 (0.372)	-0.03 (0.300)	<b>-0.15</b> (0.000)
<b>RR</b>	-0.01 (0.754)	-0.01 (0.770)	<b>-0.13</b> (0.000)	<b>-0.28</b> (0.000)	<b>0.07</b> (0.041)	0.05 (0.111)	-0.01 (0.820)	<b>-0.13</b> (0.000)
<b>SS</b>	<b>-0.16</b> (0.000)	<b>-0.08</b> (0.014)	<b>0.11</b> (0.001)	<b>0.27</b> (0.000)	<b>-0.24</b> (0.000)	<b>-0.20</b> (0.000)	<b>-0.12</b> (0.000)	0.01 (0.841)
<b>CS</b>	<b>0.18</b> (0.000)	<b>0.13</b> (0.000)	-0.04 (0.265)	<b>-0.14</b> (0.000)	<b>0.22</b> (0.000)	<b>0.22</b> (0.000)	<b>0.15</b> (0.000)	<b>0.08</b> (0.022)
<b>WTS</b>	<b>0.16</b> (0.000)	<b>0.08</b> (0.012)	<b>-0.11</b> (0.001)	<b>-0.27</b> (0.000)	<b>0.24</b> (0.000)	<b>0.21</b> (0.000)	<b>0.12</b> (0.000)	0.00 (0.884)
<b>PM</b>	<b>0.14</b> (0.000)	<b>0.15</b> (0.000)	<b>0.09</b> (0.007)	<b>0.11</b> (0.001)	<b>0.10</b> (0.003)	<b>0.15</b> (0.000)	<b>0.14</b> (0.000)	<b>0.17</b> (0.000)

The data indicates at both the family and individual tree level that tracheid diameter tends to increase with an increase in tracheid length (Table 6.8). This is expected as longer tracheids are less likely to be represented by cut ends in the samples. Although some of the individual tree correlations between cell wall thickness and tracheid length are statistically significant, for practical purposes they appear to be independent. The family mean correlations with mean tracheid area and number of tracheids per square millimetre follow a similar trend to the individual tree correlations (Tables 6.7 and 6.8).

**Table 6.8** Family mean phenotypic correlations between tracheid length and tracheid cross-sectional properties (n=109). Significant correlations in bold, p-values in brackets.

	Ring 4	Ring 6	Ring 8	Ring 10	MAge4	MAge6	MAge8	MAge10
<b>RD</b>	0.16 (0.095)	0.14 (0.139)	0.12 (0.211)	<b>0.21</b> (0.032)	0.19 (0.051)	<b>0.21</b> (0.033)	0.18 (0.068)	<b>0.20</b> (0.035)
<b>TD</b>	<b>0.24</b> (0.013)	<b>0.22</b> (0.024)	<b>0.20</b> (0.036)	<b>0.24</b> (0.014)	<b>0.29</b> (0.002)	<b>0.32</b> (0.001)	<b>0.30</b> (0.001)	<b>0.31</b> (0.001)
<b>LD</b>	<b>0.21</b> (0.031)	0.16 (0.104)	0.17 (0.079)	<b>0.21</b> (0.033)	<b>0.26</b> (0.006)	<b>0.26</b> (0.006)	<b>0.24</b> (0.011)	<b>0.25</b> (0.008)
<b>WA</b>	0.13 (0.174)	0.18 (0.062)	0.11 (0.242)	<b>0.21</b> (0.032)	0.15 (0.111)	<b>0.21</b> (0.031)	0.18 (0.069)	<b>0.20</b> (0.037)
<b>WT</b>	-0.02 (0.874)	0.10 (0.324)	0.00 (0.964)	0.07 (0.473)	-0.07 (0.501)	0.01 (0.919)	0.00 (0.965)	0.02 (0.853)
<b>TArea</b>	<b>0.19</b> (0.047)	0.17 (0.076)	0.15 (0.112)	<b>0.22</b> (0.020)	<b>0.23</b> (0.015)	<b>0.25</b> (0.008)	<b>0.23</b> (0.018)	<b>0.25</b> (0.009)
<b>NoTrach</b>	<b>-0.22</b> (0.023)	<b>-0.20</b> (0.039)	-0.17 (0.075)	<b>-0.22</b> (0.021)	<b>-0.25</b> (0.010)	<b>-0.28</b> (0.004)	<b>-0.25</b> (0.008)	<b>-0.27</b> (0.005)
<b>PCell</b>	-0.18 (0.065)	-0.09 (0.374)	-0.16 (0.096)	-0.11 (0.237)	<b>-0.25</b> (0.010)	<b>-0.21</b> (0.029)	<b>-0.21</b> (0.029)	<b>-0.20</b> (0.040)
<b>RR</b>	-0.16 (0.102)	-0.08 (0.422)	-0.13 (0.172)	-0.12 (0.210)	<b>-0.23</b> (0.016)	<b>-0.20</b> (0.036)	<b>-0.19</b> (0.044)	<b>-0.19</b> (0.049)
<b>CS</b>	0.15 (0.126)	0.13 (0.194)	0.09 (0.344)	<b>0.20</b> (0.040)	<b>0.24</b> (0.011)	<b>0.24</b> (0.013)	<b>0.20</b> (0.037)	<b>0.22</b> (0.025)
<b>SS</b>	-0.09 (0.340)	-0.07 (0.478)	-0.03 (0.768)	-0.15 (0.125)	<b>-0.22</b> (0.023)	<b>-0.19</b> (0.047)	-0.15 (0.111)	-0.16 (0.101)
<b>WTS</b>	0.09 (0.362)	0.07 (0.488)	0.03 (0.793)	0.14 (0.141)	<b>0.21</b> (0.026)	0.19 (0.051)	0.15 (0.123)	0.15 (0.111)
<b>PM</b>	<b>0.19</b> (0.043)	0.17 (0.071)	0.15 (0.110)	<b>0.22</b> (0.020)	<b>0.23</b> (0.015)	<b>0.26</b> (0.008)	<b>0.23</b> (0.017)	<b>0.25</b> (0.009)

### 6.3 Additive genetic correlations

Phenotypic correlations between two traits can easily be computed. A phenotypic correlation is caused by genetic and environmental correlations between two traits (Falconer, 1981). Of particular interest and utility in breeding programs is an

understanding of the correlation of breeding values or the additive genetic correlation between two traits.

A genetic correlation between two traits may result from either of the following:

- i) Linkage disequilibrium
- ii) Pleiotropic effects whereby a gene locus or loci influence two traits simultaneously; this is most important when considering artificial selection.
- iii) Genetic drift.

(Falconer, 1981).

In an applied breeding program, additive genetic correlations are important for predicting correlated responses, developing selection indices and comparing direct and correlated responses to determine the efficiency of selection. Wood properties are time consuming and expensive to measure, therefore in any selection program for wood properties, these additive genetic correlations are extremely important.

Additive genetic correlations were estimated for paired traits where the individual heritability of each individual trait was greater than 0.10. Traits with a heritability of less than 0.10 are not likely to be included in a breeding program and were, therefore, not considered. Estimates of genetic correlations generally have very large sampling errors. As a result, standard errors of the additive genetic correlation estimates are generally large, and in many cases they may exceed the correlation in magnitude (Tables 6.9 to 6.11). In Chapter 7 these estimates will be used to predict correlated responses and compare direct and correlated responses to selection.

### **6.3.1 Additive genetic correlations between growth and wood property traits.**

For the population of trees selected for this study only diameter at breast height (DBH) had a individual heritability greater than 0.10, therefore it was the only growth

trait considered when calculating genetic correlations. All additive genetic correlation estimates between growth (DBH) and wood density traits were negative, varying in magnitude from -0.46 to -0.12 (Table 6.9).

**Table 6.9** Additive genetic correlations between diameter at breast height and wood property traits.

<b>DBH</b>	
<b>Wood Density</b>	
<b>WMD</b>	-0.46 ± 0.22
<b>MEWD</b>	-0.26 ± 0.22
<b>MLWD</b>	-0.24 ± 0.27
<b>PLW</b>	-0.12 ± 0.29
<b>Tracheid Length</b>	
<b>Ring 6</b>	-0.26 ± 0.34
<b>Ring 10</b>	-0.09 ± 0.41
<b>Tracheid Cross-sectional properties</b>	
<b>RD</b>	-0.08 ± 0.23
<b>TD</b>	-0.07 ± 0.28
<b>LD</b>	0.07 ± 0.26
<b>WA</b>	-0.36 ± 0.27
<b>TArea</b>	-0.08 ± 0.24
<b>NoTrach</b>	0.01 ± 0.24
<b>CS</b>	-0.31 ± 0.22
<b>SS</b>	0.54 ± 0.19
<b>WTS</b>	-0.45 ± 0.21
<b>PM</b>	-0.07 ± 0.24

Unfavourable negative correlations of a similar magnitude have been reported for *P. patula* grown in Mexico. Growth and wood traits were estimated in a six-year-old *P. patula* half-sib progeny trial grown in Zacualpan, Veracruz, Mexico (Valencia-Manzo and Vargas-Hernandez, 2001). Additive genetic correlations between height, diameter, tree volume and biomass were reported to range from -0.07 to -0.36 (Valencia-Manzo and Vargas-Hernandez, 2001). It has also been reported that fast growth was negatively correlated to wood density in *P. patula* grown in Zimbabwe (Birks and Barnes, 1991). Estimates ranged from 0.37 to -1.13 and most were

negative. Gwaze et al. (2001) have also reported that genetic correlations between growth and wood density traits in loblolly pine were consistently unfavourable. Pswarayi (1993) reported that correlations between wood density and diameter or tree volume were negative, ranging from -0.11 to -0.23 in three tests of 15-year-old *P. elliotii* grown in Zimbabwe.

Additive genetic correlations between tree diameter and tracheid length were also negative but weaker (Table 6.9). Associated standard errors were large due to the low levels of additive variance at the family level. General indications are that selection for diameter growth is likely to have an adverse effect on tracheid length, but this will be minimal. Other than cell wall area, all the CSIR measured and derived tracheid cross-sectional traits were weakly correlated with diameter growth (CSIR). Associated standard errors generally exceeded the additive genetic correlation estimates. SilviScan® derived tracheid cross-sectional traits were mostly moderately correlated with diameter growth.

### **6.3.2 Additive genetic correlations between wood density and tracheid length and cross-sectional traits.**

The additive genetic correlation estimates between wood density traits and tracheid length for rings six and ten were variable in magnitude and direction, ranging from -0.03 to -1.34 (Table 6.10). The results are therefore difficult to interpret. For example, the genetic correlation between mean latewood density and tracheid length for ring six was 0.37 and with tracheid length for ring ten -0.19. This inconsistency is likely to be due to sampling error. The genetic correlation between core weighted mean wood density and tracheid length was consistently negative but also varied in magnitude (Table 6.10). From the results, it could be expected that selection for wood density might have a slight negative effect on tracheid length.

**Table 6.10** Additive genetic correlations between wood density and tracheid traits.

	WMD	MEWD	MLWD	PLW
<b>Tracheid Length</b>				
<b>R6</b>	-0.40 ± 0.20	-0.36 ± 0.18	0.37 ± 0.21	-0.03 ± 0.25
<b>R10</b>	-0.06 ± 0.27	0.05 ± 0.23	-0.19 ± 0.27	-1.34 ± 0.23
<b>Tracheid Cross-sectional properties</b>				
<b>RD</b>	-0.30 ± 0.14	-0.12 ± 0.14	-0.42 ± 0.14	-0.21 ± 0.17
<b>TD</b>	-0.35 ± 0.16	-0.11 ± 0.18	-0.56 ± 0.15	-0.03 ± 0.22
<b>LD</b>	-0.46 ± 0.14	-0.27 ± 0.15	-0.39 ± 0.17	-0.35 ± 0.18
<b>WA</b>	-0.12 ± 0.20	0.14 ± 0.19	-0.71 ± 0.12	1.35 ± 0.19
<b>TArea</b>	-0.25 ± 0.15	-0.08 ± 0.15	-0.42 ± 0.15	-0.11 ± 0.19
<b>NoTrach</b>	0.28 ± 0.15	0.11 ± 0.15	0.46 ± 0.15	0.11 ± 0.19
<b>CS</b>	0.19 ± 0.16	0.34 ± 0.14	-0.45 ± 0.15	0.33 ± 0.17
<b>SS</b>	-0.56 ± 0.12	-0.63 ± 0.10	0.36 ± 0.17	-0.65 ± 0.12
<b>WTS</b>	0.55 ± 0.12	0.64 ± 0.10	-0.37 ± 0.17	0.65 ± 0.12
<b>PM</b>	-0.32 ± 0.15	-0.12 ± 0.15	-0.48 ± 0.14	-0.15 ± 0.18

Genetic correlations between wood density and tracheid cross-sectional traits were almost all negative, the same direction as the phenotypic correlations between these traits, and generally larger in magnitude. Standard error estimates were reasonable. Similar magnitude additive genetic correlations between wood density and radial ( $r_A = -0.41$ ) and tangential ( $r_A = -0.61$ ) tracheid diameter were reported by Shelbourne et al. (1997) for *P. radiata*. Overall selection for any wood density trait is likely to result in a slight reduction in tracheid diameter.

SilviScan® derived cell wall thickness was strongly and positively correlated ( $r_A = 0.55$  and  $0.64$ ) with core area weighted mean wood density and mean earlywood density. Nyakuengama et al. (1999) reported a genetic correlation of  $0.58$ , and Shelbourne et al. (1997) a genetic correlation of  $0.71$  between cell wall thickness and area weighted mean core density. These studies are in good agreement with this study.

### 6.3.3 Additive genetic correlations between tracheid length and cross-sectional traits.

The author is not aware of any other published genetic correlation estimates between tracheid length and tracheid cross-sectional properties. Additive genetic correlations were on the whole moderate and positive between tracheid traits (Table 6.11).

**Table 6.11** Additive genetic correlations between tracheid length and tracheid cross-sectional properties.

	Ring 6	Ring 10
<b>RD</b>	0.25 ± 0.22	0.32 ± 0.22
<b>TD</b>	0.19 ± 0.26	0.53 ± 0.22
<b>LD</b>	0.11 ± 0.25	0.26 ± 0.27
<b>WA</b>	0.39 ± 0.25	0.49 ± 0.25
<b>TArea</b>	0.24 ± 0.22	0.45 ± 0.21
<b>NoTrach</b>	0.07 ± 0.24	0.37 ± 0.23
<b>CS</b>	0.21 ± 0.23	0.74 ± 0.12
<b>SS</b>	-0.04 ± 0.25	-0.81 ± 0.10
<b>WTS</b>	0.12 ± 0.25	0.76 ± 0.12
<b>PM</b>	0.31 ± 0.21	0.44 ± 0.21

The exception to this was the correlation between tracheid length and specific surface. This provides evidence that the same genes control both tracheid length and tracheid cross-sectional traits. In all cases, the magnitude of the correlation increased with age, from ring six to ring 10.

## 6.4 Conclusions

At the individual tree level, only five of the 25 correlations computed between tree volume and wood property traits were statistically significant. Correlations with tree diameter were also weak, although most with tracheid cross-sectional properties were statistically significant. Trees for this study were selected on the basis of their size or individual tree volume. An underlying assumption was that the growth and

wood properties are independent and that by selecting better trees no bias would be introduced that would affect the estimation of wood property parameters. Indications from the data are that this was a valid assumption.

For practical purposes tracheid length in *P. patula* appears to be independent of all wood density traits evaluated in this study. Trees with higher overall density tend to have smaller diameter tracheids, while at the family level families with higher mean earlywood density also have larger diameter tracheids. This correlation is probably driven by the var. *longipedunculata* provenances from southern Mexico that tended to have larger diameter tracheids and higher density earlywood (reported on in Chapter 5).

Other published reports support the finding in this study that wood density is genetically negatively correlated with diameter growth. The magnitude of the additive genetic correlation between weighted mean density at breast height and diameter growth is likely to have had a negative impact on overall wood density. This finding is one of the most important to emerge in this chapter. The impact of this adverse correlation in a breeding program will be quantified in the next chapter of this thesis.

## Chapter 7

### Predicted Genetic Gains, Correlated Responses to Selection, Practical Recommendations and Final Summary

#### 7.1 Predicted genetic gains

If a breeder wanted to establish a specialized clonal seed orchard for a particular wood property, 20 unrelated selections would be close to the ideal number. This would allow for sufficient out-crossing and some culling. Using this as a criterion a selection intensity of two percent or one-in-50 was used to calculate predicted gains. This is based on the assumption that the 20 best individuals would be selected from the population used in this study. This equates to a selection intensity ( $i$ ) of 2.421. Only wood property traits where the individual heritability exceeded 0.10 were considered. It is unlikely that any trait with an individual heritability of less than 0.10 would be included in a breeding program.

Typically, gains per selection cycle for growth traits in pines range from 10 to 30 percent (Talbert *et al.*, 1985; Wright *et al.*, 1996 and Li *et al.*, 1999). Larger populations of trees can be assessed for growth traits, as they are cheaper and easier to assess and more intense selection can be practised. Typically each family in a progeny trial would be represented by anywhere between 25 and 30 progeny. Therefore, if 108 families were included this would translate to between 2700 and 3240 trees. Applying the same criteria of selecting 20 trees for a clonal seed orchard, the selection intensity for growth traits would be between 2.76 and 2.82. In reality, because of the high cost of assessing wood properties, smaller populations of trees will be assessed. As a result, less intensive selection will be able to be practised. This will have an impact on the magnitude of realized gains.

Predicted gains based on selecting the top 20 individual trees from this population ranged from one percent to 22 percent (Table 7.1). The predicted gains of three and one percent for tracheid length are not meaningful as this equates to an absolute increase of 0.08 mm and 0.06 mm respectively (Table 7.1). An increase of this magnitude would have no practical benefit.

**Table 7.1** Gain predictions for direct selection on wood property traits, assuming a selection intensity of one-in-50 ( $i = 2.421$ ).

Trait	$h^2$ Trait	$\sigma^2_{\text{phen}}$ Trait	Mean	Actual Gain	% Gain
<b>WMD</b>	0.27	0.001232	0.443	0.023	5%
<b>MEWD</b>	0.37	0.000394	0.366	0.018	5%
<b>MLWD</b>	0.26	0.000683	0.611	0.016	3%
<b>PLW</b>	0.25	89.93	25.76	5.74	22%
<b>Ring 6</b>	0.13	0.06451	2.72	0.08	3%
<b>Ring 10</b>	0.10	0.06851	4.25	0.06	1%
<b>RD</b>	0.52	7.39	41.33	3.42	8%
<b>TD</b>	0.27	3.04	34.85	1.14	3%
<b>LD</b>	0.35	3.58	26.51	1.60	6%
<b>WA</b>	0.20	3559.04	504.92	28.89	6%
<b>TArea</b>	0.45	245640.8	4534	539.95	12%
<b>NoTrach</b>	0.40	587.78	224.06	23.48	10%
<b>CS</b>	0.44	5417.97	626.84	78.41	13%
<b>WTS</b>	0.31	0.0535	2.74	0.17	6%
<b>SS</b>	0.30	435.48	246.16	15.16	6%
<b>PM</b>	0.45	70.13	152.25	9.12	6%

Predicted gains for wood density traits range from three to 22 percent. There may be some advantage from a wood uniformity point of view to select for increased mean earlywood density. It may be possible to narrow the range between mean earlywood density and mean latewood density without a dramatic increase in latewood density. This will depend on the correlated response in the latewood and will be discussed in the next section.

Tracheid cross-sectional properties will also respond to selection, as will the associated derived traits, mean tracheid area and mean number of tracheids per square millimetre (Table 7.1). These may be extremely important traits if a strong link exists between them and paper properties. A follow-up study is planned to quantify this. Moderate gains are also possible with the SilviScan® derived traits as they have been termed in this thesis. They are also likely to have a significant impact on paper properties (Kibblewhite, 1999).

## **7.2 Correlated responses to selection**

A further problem for consideration in an applied breeding program concerns the response to selection: if a breeder selects for trait "X", what will be the change in the correlated character "Y"? The response of a correlated character can be predicted if the genetic correlation and the heritabilities of the two traits are known. Typically, if the genetic correlation is low, close agreement between the observed and predicted correlated responses is not often found (Falconer, 1981). In the absence of the information required to be able to predict correlated responses, breeders may inadvertently select against a desirable characteristic. Because wood property data is expensive to acquire and tree populations need to be large to estimate the required genetic parameters, few studies have reported on correlated responses to selection in wood properties. The same selection intensity of one-in-50 that was used to predict direct responses to selection, was also used to predict the correlated responses.

### **7.2.1 Response among wood property traits to direct selection for increased tree diameter growth.**

In the previous chapter the existence of unfavorable negative additive genetic correlations between diameter growth and wood properties were highlighted. The question must be asked, "What have we been doing to the wood properties by

selecting for improved growth?". To quantify this, the potential impacts of these unfavourable correlations in a breeding program were predicted.

The individual heritability estimate for diameter growth, calculated using this population of trees (see Chapter 6), is biased because the best tree was chosen in each plot to be sampled. Kanzler (2002), calculated single site heritabilities for the Maxwell site in his genotype by environment interaction study. The mean single-site heritability estimate from that study ( $h^2 = 0.18$  for diameter growth), calculated using all trees planted in the study, and eight year growth data, is likely to have less bias and was used in this study to predict the correlated responses to selection.

Selection for tree diameter alone will have a negative effect on all density traits (Table 7.2). Because tree diameter makes up a large component of total tree volume, selection for tree growth alone is likely to have had a slight negative effect on the wood density of advanced generation material that is being deployed operationally. This could offer a possible explanation as to why the second generation control seedlot (SA control) included in this study had lower than average wood density (see Chapter 3). The SA control had a weighted mean core density of  $0.435 \text{ g cm}^{-3}$ , which is approximately two percent below the population mean for this study.

In real terms, the magnitude of the responses among the density traits are small, but the breeder needs to be aware that selection for growth alone is likely to lead to a reduction in wood density over time (Table 7.2).

Selection for diameter growth is not likely to result in any change in tracheid length of practical significance. Tracheid length generally exceeds the critical level in *P. patula*. Similarly, although negative, responses in tracheid dimensions are negligible (Table 7.2). Selection for increased diameter growth is likely to result in a small increase in specific surface, derived using the SilviScan® approach.

**Table 7.2** Predicted correlated responses among wood property traits for direct selection on tree diameter growth.

Trait 1	$h^2$ Trait 1	Trait 2	$h^2$ Trait 2	$r_A$	$\sigma^2_{phen}$ Trait 2	Response (Actual)	Mean (Base pop.)	% of Mean Trait 2
<b>DBH</b>	0.18	<b>WMD</b>	0.27	-0.46	0.001232	-0.009	0.443	-2%
	0.18	<b>MEWD</b>	0.37	-0.26	0.000394	-0.003	0.366	-1%
	0.18	<b>MLWD</b>	0.26	-0.24	0.000683	-0.003	0.611	-1%
	0.18	<b>PLW</b>	0.25	-0.12	89.93	-0.58	25.76	-2%
<b>DBH</b>	0.18	<b>Ring 6</b>	0.13	-0.26	0.06451	-0.02	2.72	-1%
	0.18	<b>Ring 10</b>	0.10	-0.09	0.06851	-0.01	4.25	0%
<b>DBH</b>	0.18	<b>RD</b>	0.52	-0.08	7.39	-0.16	41.33	0%
	0.18	<b>TD</b>	0.27	-0.07	3.04	-0.07	34.85	0%
	0.18	<b>LD</b>	0.35	0.07	3.58	0.08	26.51	0%
	0.18	<b>WA</b>	0.20	-0.36	3559.04	-9.87	504.92	-2%
	0.18	<b>TArea</b>	0.45	-0.08	245640.80	-27.32	4534	-1%
	0.18	<b>NoTrach</b>	0.40	0.01	587.78	0.16	224.06	0%
	0.18	<b>CS</b>	0.44	-0.31	5417.97	-15.55	626.84	-2%
	0.18	<b>WTS</b>	0.31	-0.45	0.05	-0.060	2.74	-2%
	0.18	<b>SS</b>	0.30	0.54	435.48	6.340	246.16	3%
	0.18	<b>PM</b>	0.45	-0.07	70.13	-0.40	152.25	0%

It can be concluded that, even at the genetic level tracheid dimensions are independent of tree diameter growth. The two traits do not appear to be affected by the same physiological pathways or functions, and are likely determined by different sets of genes. If the size and number of tracheids are an important determinant of paper quality, then selection for increased growth is unlikely to have changed these traits.

### 7.2.2 Response among wood property traits to direct selection for area weighted mean density

Among wood properties of interest, area weighted mean wood density at breast height is one of the easiest and cheapest to measure. The importance of wood density has been reviewed in Chapter 3. To briefly summarize, most wood density

studies in pines have shown that wood density has a direct effect on pulp yield and paper strength, and on strength and utility of solid wood products (Zobel and Jett, 1995). Van Buijtenen (1967) found that increased wood density and latewood percent results in paper with greater tear strength but in decreased tensile and bursting strengths. Similarly, a large proportion of low density juvenile wood results in low tear and high burst and tensile strength. Undoubtedly, many breeding programs include wood density as a selection criteria in their breeding programs. It is important to understand what effect selection for wood density could have on tracheid properties. Correlated responses were calculated and are presented in Table 7.3.

As expected, selection to increase wood density will lead to a slight reduction (3%) in tree diameter growth (Table 7.3). This sacrifice may be worth a five percent increase in wood density. The response in mean earlywood density to selection on core weighted mean wood density is also favorable, while there is very little change in mean latewood density (Table 7.3). It should be possible to increase the overall wood density with a positive correlated response in mean earlywood density and maintain mean latewood density relatively constant (Table 7.3). This could lead to more uniform pith-to-bark density profiles that should benefit the processor.

Selection for increased wood density will lead to a slight reduction in tracheid size and length (radial, tangential and lumen diameter). As a result of this, the mean number of tracheids per unit of wood will increase slightly (Table 7.3). As mentioned previously, the numbers and dimensions of the tracheids could have a profound effect on paper properties. For example, for a softwood pulp, long fibers and high relative numbers of fibers together are critical to achieve good web reinforcement and formation in low grammage grades (Kibblewhite, 1999). This needs to be quantified in a further study using trees measured for this study, as the complete range of wood properties has been measured on a per tree basis.

**Table 7.3** Predicted correlated responses among growth and wood property traits for direct selection on core weighted mean wood density.

Trait 1	$h^2$	Trait 2	$h^2$	$r_A$	$\sigma^2_{phen}$	Response	Mean	% of Mean
	Trait 1		Trait 2		Trait 2	(Actual)	(Base pop.)	Trait 2
<b>WMD</b>	0.27	<b>DBH</b>	0.18	-0.46	8.61521	-0.721	25.04	-3%
<b>WMD</b>	0.27	<b>MEWD</b>	0.37	0.85	0.000394	0.013	0.366	4%
	0.27	<b>MLWD</b>	0.26	0.12	0.000683	0.002	0.611	0%
	0.27	<b>PLW</b>	0.25	0.95	89.93	5.667	25.76	22%
<b>WMD</b>	0.27	<b>Ring 6</b>	0.13	-0.40	0.06451	-0.046	2.72	-2%
	0.27	<b>Ring 10</b>	0.10	-0.06	0.06851	-0.006	4.25	0%
<b>WMD</b>	0.27	<b>RD</b>	0.52	-0.30	7.39	-0.740	41.33	-2%
	0.27	<b>TD</b>	0.27	-0.35	3.04	-0.399	34.85	-1%
	0.27	<b>LD</b>	0.35	-0.46	3.58	-0.648	26.51	-2%
	0.27	<b>WA</b>	0.20	-0.12	3559.04	-4.028	504.92	-1%
	0.27	<b>TArea</b>	0.45	-0.25	245640.8	-104.562	4534	-2%
	0.27	<b>NoTrach</b>	0.40	0.28	587.78	5.401	224.06	2%
	0.27	<b>CS</b>	0.44	0.19	5417.97	11.670	626.84	2%
	0.27	<b>WTS</b>	0.31	0.55	0.0535	0.089	2.74	3%
	0.27	<b>SS</b>	0.30	-0.56	435.48	-8.052	246.16	-3%
	0.27	<b>PM</b>	0.45	-0.32	70.13	-2.261	152.25	-1%

### 7.2.3 Response among wood property traits to direct selection for mean earlywood density.

So far, none of the components of wood density, of which earlywood density is one, have been reported to have a higher heritability than overall density, and these components have had limited value in improving selection efficiency for overall density (Zobel and Jett, 1995). However, in this study, the heritability estimate for mean earlywood density ( $h^2 = 0.37$ ) was considerably higher than the estimate for weighted mean density ( $h^2 = 0.27$ ) (see Chapter 3). Therefore, it may be more appropriate to select for increased earlywood density in trees grown on short pulpwood rotation as this component of overall density has a higher heritability and makes up a large proportion of the tree trunk.

The correlated responses for diameter growth and wood property traits were predicted (Table 7.4). Direct selection to increase mean earlywood density will result in a slight decrease in diameter growth (2%), and an increase in core weighted mean density (5%) and mean percentage of latewood (24%). The predicted correlated response for weighted mean density is the same as the response expected from direct selection on this trait (Table 7.1). By selecting for mean earlywood density, a five percent response is expected for both traits. Alternatively, if direct selection is applied to increase weighted mean density, the correlated response in earlywood density is slightly less at four percent (Table 7.3). There is some merit in selecting for increased earlywood density as a primary wood property trait, no loss in overall density is likely, and uniformity is an added benefit.

**Table 7.4** Predicted correlated responses among growth and wood property traits for direct selection on core mean earlywood density.

Trait 1	$h^2$	Trait 2	$h^2$	$r_A$	$\sigma^2_{phen}$	Response	Mean	% of Mean
	Trait 1		Trait 2		Trait 2	(Actual)	(Base pop.)	Trait 2
<b>MEWD</b>	0.37	<b>DBH</b>	0.18	-0.26	8.61521	-0.477	25.04	-2%
<b>MEWD</b>	0.37	<b>WMD</b>	0.27	0.85	0.001232	0.023	0.443	5%
	0.37	<b>MLWD</b>	0.26	-0.39	0.000683	-0.008	0.611	-1%
	0.37	<b>PLW</b>	0.25	0.89	89.93	6.215	25.76	24%
<b>MEWD</b>	0.37	<b>Ring 6</b>	0.13	-0.36	0.06451	-0.049	2.72	-2%
	0.37	<b>Ring 10</b>	0.10	0.05	0.06851	0.006	4.25	0%
<b>MEWD</b>	0.37	<b>RD</b>	0.52	-0.12	7.39	-0.346	41.33	-1%
	0.37	<b>TD</b>	0.27	-0.11	3.04	-0.147	34.85	0%
	0.37	<b>LD</b>	0.35	-0.27	3.58	-0.445	26.51	-2%
	0.37	<b>WA</b>	0.20	0.14	3559.04	5.501	504.92	1%
	0.37	<b>TArea</b>	0.45	-0.08	245640.8	-39.169	4534	-1%
	0.37	<b>NoTrach</b>	0.40	0.11	587.78	2.484	224.06	1%
	0.37	<b>CS</b>	0.44	0.34	5417.97	24.447	626.84	4%
	0.37	<b>WTS</b>	0.31	0.64	0.0535	0.121	2.74	4%
	0.37	<b>SS</b>	0.30	-0.63	435.48	-10.604	246.16	-4%
	0.37	<b>PM</b>	0.45	-0.12	70.13	-0.993	152.25	-1%

Selection to increase mean earlywood density is also likely to have a positive impact on cell wall thickness (SilviScan® derived) and coarseness (Table 7.4). Coarseness may also be an important determinant of paper property. The slight negative responses for the other wood property traits are small and not likely to be of practical significance. Selecting on mean earlywood density is likely to have less of an impact on the tracheid dimensions (RD, TD and LD), than direct selection on weighted mean density (Table 7.3 and Table 7.4).

#### **7.2.4 Response among wood property traits to direct selection for increased tracheid radial diameter.**

Tracheid radial diameter is the tracheid cross-sectional and wood property with the highest individual tree heritability. Although not cheap and easy to measure, as it requires an image analysis system, it could be included in a selection program if it can be demonstrated that it plays an important role in determining paper properties. The additive genetic correlations between radial tracheid diameter and other tracheid cross-sectional properties were also very strong and positive (see Chapter 5). Because of its high heritability, it is an attractive trait for inclusion into a selection program.

Earlier in this chapter, a predicted genetic gain of eight percent from direct selection was reported for tracheid radial diameter. Correlated responses among tree diameter growth, wood density, tracheid length and other tracheid diameter traits were predicted (Table 7.5). If deemed important, any selection program to increase tracheid radial diameter is likely to result in a small reduction, ranging from one to two percent, in diameter growth and wood density (Table 7.5). The response in tracheid length is small, but positive, while other tracheid cross-section dimensions will also increase.

The response to selection on tracheid radial diameter will lead to a larger response in tracheid tangential and lumen diameter than direct selection for these traits (Table 7.1 and Table 7.5). This is driven by the substantially higher heritability estimate for radial tracheid diameter and is a good example of how indirect selection can be more efficient than direct selection. Similarly, if more, smaller diameter tracheids are desirable for a required product, an increase in wood density can be expected. Gains will be of a similar magnitude.

**Table 7.5** Predicted correlated responses among growth and wood property traits for direct selection on mean tracheid radial diameter.

Trait 1	$h^2$	Trait 2	$h^2$	$r_A$	$\sigma^2_{phen}$	Response	Mean	% of Mean
	Trait 1		Trait 2		Trait 2	(Actual)	(Base pop.)	Trait 2
RD	0.52	DBH	0.18	-0.08	8.61521	-0.174	25.04	-1%
RD	0.52	WMD	0.27	-0.30	0.001232	-0.010	0.443	-2%
	0.52	MEWD	0.37	-0.12	0.000394	-0.003	0.366	-1%
	0.52	MLWD	0.26	-0.42	0.000683	-0.010	0.611	-2%
	0.52	PLW	0.25	-0.21	89.93	-1.738	25.76	-7%
RD	0.52	Ring 6	0.13	0.25	0.06451	0.040	2.72	1%
	0.52	Ring 10	0.10	0.32	0.06851	0.046	4.25	1%
RD	0.52	TD	0.27	0.92	3.04	1.455	34.85	4%
	0.52	LD	0.35	0.96	3.58	1.876	26.51	7%
	0.52	WA	0.20	1.00	3559.04	46.578	504.92	9%

### 7.3 Practical recommendations

#### 7.3.1 Conservation of germplasm

One of the most important questions that this study was designed to answer was, “Are provenance differences important for wood properties?” The results have highlighted the importance of provenance effects in *P. patula*. In particular, the differences between var. *patula* and var. *longipedunculata* in wood density and

tracheid cross-sectional traits were marked. At age five and eight, selections were made throughout the *P. patula* CAMCORE trial series in South Africa. A total of 179 trees have been selected, only 26 selections (15%) were made in families of var. *longipedunculata*.

- ***Although var. longipedunculata is more sensitive to cold, this germplasm needs to be conserved and its purity maintained until the economic value of these differences in wood properties can be quantified.***

Ninety-three selections (52%) were made in families from Potrero de Monroy and Corralitla, these two provenances grew the best in South Africa. Selections have been concentrated in these two provenances that tended to have lower than average wood density and mean earlywood density.

- ***Some consideration should be given to increasing the number of selections from other provenances to maintain diversity for other wood properties.***

### **7.3.2 Wood properties to be included in a selection program**

Mean earlywood density can be measured relatively cheaply using a densitometer, it has a higher heritability than weighted mean density, and a genetic co-efficient of variation of eight percent ( $0.029 \text{ g cm}^{-3}$ ). This makes it an ideal trait to include in a selection program. Correlated responses in weighted mean density and percentage latewood are positive and similar in magnitude to those that would be expected from direct selection on these traits. Most pulp-wood is sold to mills on a per ton basis, therefore the slight predicted loss in tree diameter is not of practical importance and will be negated by a five percent improvement in wood density. The improvement in pith-to-bark uniformity is also likely to have added benefits when the tracheid is

processed. It has already been shown that increased wood density has a positive impact on some of the important paper strength properties (Zobel and Jett, 1995 and van Buijtenen, 1967).

Once quantified, it may be that the number and size of tracheids is critical for the production of particular paper grades. In this study, tracheid diameter traits have been shown to have some of the highest heritabilities. Good gains can be achieved from direct selection. However, it has been shown that selection for increased tracheid radial diameter will lead to a reduction in tree diameter and wood density. Tracheid cross-sectional traits are still expensive to measure. In this study it was 10 times more expensive to measure tracheid cross-sectional properties than wood density using a densitometer. Despite advances in technology, no applied breeding program is going to be able to routinely assess the tracheid cross-sectional properties of all candidate trees in a breeding population.

Selection on multiple traits always involves a compromise, but it may be worthwhile including wood property traits into a selection index. One option is to include expensive to measure traits in combined indices as family means only. This may be the best approach with tracheid cross-sectional traits. If prior information is available, an optimum family size to maximize the precision of genetic parameter estimates can be determined. This was discussed in Chapter 2. In this study, tracheid radial diameter had an individual heritability estimate of 0.52. In practice, eight progeny per family are likely to be sufficient to determine a reliable family mean. Depending on the economic return or value that breeding for smaller or larger diameter tracheids may have, it would be feasible to assess eight progeny from the top 50 families pre-selected for growth (i.e. 400 trees). However, for the same cost, wood density could be measured on 2000 trees.

- ***Until the possible benefits of changing the cross-sectional dimensions of *P. patula* tracheids can be quantified, it is recommended that selection to***

***increase mean earlywood density be implemented in breeding programs for *P. patula* on short pulpwood rotations. This can be achieved by including mean earlywood density in a combined index with tree growth.***

### 7.3.3 Specialist production populations

Tree breeding, particularly pine breeding, has long generation intervals. Mill requirements can change rapidly, making it difficult for breeding programs to respond to changes. Robust selection criteria are therefore required for breeding population advancement. It may be more appropriate to respond to specific raw material requirements by establishing specialist, backwards selected clonal orchards, with no more than 10-15 genotypes. Even using this approach it would take approximately 16 years (from selection stage) before a clonal orchard would be in full production.

These individuals could be selected on the basis of their family mean performance in progeny trials. Typically Sappi tests 100 open-pollinated families per progeny trial series. If it was the objective to select for smaller or larger diameter tracheids, this could be achieved by selecting the top 50 families on diameter growth, and then evaluating the tracheid cross-sectional properties of eight progeny from each family. Using the family mean data, the parents of the 10-15 best families could be grafted and used to establish a clonal seed orchard.

If the original parent trees were available from the population used in this study, gains from selecting the best 12 parents using family mean performance for mean earlywood density would be as follows:

$$\Delta G = 2h_{f(b)}^2 S_{F \text{ top } 12} \text{ where;}$$

$$h_{f(b)}^2 = 0.56$$

$S_{F \text{ top } 12} = 0.031$ , therefore

$\Delta G = 0.035 \text{ g cm}^{-3}$  or 9%.

- ***Backwards-selection, if parent trees are still available, therefore offers an attractive and reliable option to implement deployment of specific material.***

#### 7.4 Final summary

The additive genetic control of wood properties in *P. patula* ranges from weak ( $h^2 < 0.10$ ) to moderately strong ( $h^2 > 0.40$ ). Values obtained for *P. patula* are somewhat weaker than what has been reported by other authors and summarized by Zobel and Jett (1995). In this study a co-efficient on relationship between half-sibs of 0.33, not 0.25 was used, and this would lower the heritability estimates slightly. Furthermore, if provenance effects are excluded from the statistical model, then the estimates of the family variance rather than family nested within provenance variance component used to derive the genetic parameters would be higher but biased. For example, if provenance effects are ignored and a co-efficient of relationship of 0.25 is used, the individual heritability estimate for weighted mean core density would increase from 0.27 to 0.48.

Based on the results, tracheid length should not be considered for selection in a *P. patula* tree improvement program. Nevertheless, large tree-to-tree variation exists. This could be due to micro-site environmental effects, or non-additive (epistatic) gene action. If it is the latter, then it could be captured operationally when clonal forestry for *P. patula* becomes feasible. Other wood properties (discussed above) offer promising prospects for improvement, but the economic value of these changes needs to be quantified. Results have demonstrated that sufficient phenotypic variation and genetic control exists to make selection and breeding for juvenile core wood properties in *P. patula* successful.

Depending on the pairs of traits examined, additive genetic correlations are either both favorable and unfavorable and vary from weak to strong. No other studies have reported on correlations among and between wood property traits in this amount of detail. Predicted correlated responses have provided some insight into what has been happening to the wood properties as we advance our breeding populations, using growth as the main selection criteria. This could explain why the South African second generation control seedlot had lower than average density. Fortunately, the additive genetic correlations between diameter growth and tracheid dimensions are very weak, therefore continued selection for growth should have had little impact on these traits.

Density trends with age, discussed in Chapter 3, indicate that trees from some provenances and families exhibit a rapid increase in density during the last three years of growth. This could change the provenance and family rankings at rotation age, and needs to be confirmed. However, on short rotations, e.g. 16 years, the wood properties of the juvenile core, characterized in detail in this study, will have a dominant impact on whole tree properties. Any change in the juvenile wood properties is likely to have a significant impact on the quality of the raw material that we supply to our processing facilities.

Clinal trends for the wood properties assessed in this study were surprisingly strong. The robustness of these findings can easily be tested using material established in later CAMCORE *P. patula* trial series planted in South Africa. The strong trend for wood properties to vary with the latitude of the collection site should make it possible to predict what sort of wood properties can be expected from the other 11 provenances of *P. patula* that are not included in this study. This should be confirmed by sampling provenances from the extremes in the new trial series.

Advances in technology are making it possible to carry out more detailed wood property studies on larger sample sizes that are more appropriate for the accurate determination of genetic parameters. Costs of assessing tracheid cross-sectional properties still remain high. To be included routinely in breeding programs the economic value of any changes to these traits needs to be demonstrated. Therefore, it is critically important to investigate the relationship between wood properties and the pulp and paper properties in more detail. This will be easier now that the wood properties can be characterized on a larger scale and is a vital step in quantifying the benefits that may accrue from changes to wood anatomy in pines.

Studies are underway in South Africa to develop calibration models to predict wood chemical composition from near-infrared (NIR) spectra. The other half of the cores used in this study have been stored and will be used to characterize the wood chemical composition of this population once the development of the calibration models has been completed.

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## Appendices

### Appendix 1. Families included in the study.

Site	Trial	Species	Provenance	Family
Maxwell	20-07-01L	<i>P. patula</i>	Potrero de Monroy	2
Maxwell	20-07-01L	<i>P. patula</i>	Potrero de Monroy	7
Maxwell	20-07-01L	<i>P. patula</i>	Potrero de Monroy	8
Maxwell	20-07-01L	<i>P. patula</i>	Potrero de Monroy	9
Maxwell	20-07-01L	<i>P. patula</i>	Potrero de Monroy	12
Maxwell	20-07-01L	<i>P. patula</i>	Potrero de Monroy	14
Maxwell	20-07-01L	<i>P. patula</i>	Potrero de Monroy	21
Maxwell	20-07-01L	<i>P. patula</i>	Potrero de Monroy	22
Maxwell	20-07-01L	<i>P. patula</i>	Potrero de Monroy	26
Maxwell	20-07-01L	<i>P. patula</i>	Ingenio del Rosario	38
Maxwell	20-07-01L	<i>P. patula</i>	Ingenio del Rosario	41
Maxwell	20-07-01L	<i>P. patula</i>	Ingenio del Rosario	44
Maxwell	20-07-01L	<i>P. patula</i>	Ingenio del Rosario	45
Maxwell	20-07-01L	<i>P. patula</i>	Ingenio del Rosario	48
Maxwell	20-07-01L	<i>P. patula</i>	Ingenio del Rosario	49
Maxwell	20-07-01L	<i>P. patula</i>	Ingenio del Rosario	50
Maxwell	20-07-01L	<i>P. patula</i>	Ingenio del Rosario	51
Maxwell	20-07-01L	<i>P. patula</i>	Ingenio del Rosario	53
Maxwell	20-07-01L	<i>P. patula</i>	Corralitla	54
Maxwell	20-07-01L	<i>P. patula</i>	Corralitla	57
Maxwell	20-07-01L	<i>P. patula</i>	Corralitla	63
Maxwell	20-07-01L	<i>P. patula</i>	Corralitla	64
Maxwell	20-07-01L	<i>P. patula</i>	Corralitla	66
Maxwell	20-07-01L	<i>P. patula</i>	Corralitla	67
Maxwell	20-07-01L	<i>P. patula</i>	Corralitla	69
Maxwell	20-07-01L	<i>P. patula</i>	Corralitla	73
Maxwell	20-07-01L	<i>P. patula</i>	Corralitla	74
Maxwell	20-07-02D	<i>P. patula</i>	El Manzanal	78
Maxwell	20-07-02D	<i>P. patula</i>	El Manzanal	80
Maxwell	20-07-02D	<i>P. patula</i>	El Manzanal	85
Maxwell	20-07-02D	<i>P. patula</i>	El Manzanal	86
Maxwell	20-07-02D	<i>P. patula</i>	El Manzanal	88
Maxwell	20-07-02D	<i>P. patula</i>	El Manzanal	90
Maxwell	20-07-02D	<i>P. patula</i>	El Manzanal	95
Maxwell	20-07-02D	<i>P. patula</i>	El Manzanal	100
Maxwell	20-07-02D	<i>P. patula</i>	El Manzanal	102
Maxwell	20-07-02D	<i>P. patula</i>	El Tlacuache	107
Maxwell	20-07-02D	<i>P. patula</i>	El Tlacuache	119
Maxwell	20-07-02D	<i>P. patula</i>	El Tlacuache	121
Maxwell	20-07-02D	<i>P. patula</i>	El Tlacuache	123

<b>Site</b>	<b>Trial</b>	<b>Species</b>	<b>Provenance</b>	<b>Family</b>
Maxwell	20-07-02D	<i>P. patula</i>	El Tlacuache	124
Maxwell	20-07-02D	<i>P. patula</i>	El Tlacuache	125
Maxwell	20-07-02D	<i>P. patula</i>	El Tlacuache	128
Maxwell	20-07-02D	<i>P. patula</i>	El Tlacuache	130
Maxwell	20-07-02D	<i>P. patula</i>	El Tlacuache	131
Maxwell	20-07-02D	<i>P. patula</i>	Ixtlan	138
Maxwell	20-07-02D	<i>P. patula</i>	Ixtlan	141
Maxwell	20-07-02D	<i>P. patula</i>	Ixtlan	145
Maxwell	20-07-02D	<i>P. patula</i>	Ixtlan	147
Maxwell	20-07-02D	<i>P. patula</i>	Ixtlan	148
Maxwell	20-07-02D	<i>P. patula</i>	Ixtlan	150
Maxwell	20-07-02D	<i>P. patula</i>	Ixtlan	153
Maxwell	20-07-02D	<i>P. patula</i>	Ixtlan	154
Maxwell	20-07-02D	<i>P. patula</i>	Ixtlan	156
Maxwell	20-07-02D	<i>P. patula</i>	Santa Maria Papalo	159
Maxwell	20-07-02D	<i>P. patula</i>	Santa Maria Papalo	160
Maxwell	20-07-02D	<i>P. patula</i>	Santa Maria Papalo	163
Maxwell	20-07-02D	<i>P. patula</i>	Santa Maria Papalo	167
Maxwell	20-07-02D	<i>P. patula</i>	Santa Maria Papalo	168
Maxwell	20-07-02D	<i>P. patula</i>	Santa Maria Papalo	169
Maxwell	20-07-02D	<i>P. patula</i>	Santa Maria Papalo	170
Maxwell	20-07-02D	<i>P. patula</i>	Santa Maria Papalo	171
Maxwell	20-07-02D	<i>P. patula</i>	Santa Maria Papalo	172
Maxwell	20-07-05L	<i>P. patula</i>	Pinal de Amoles	199
Maxwell	20-07-05L	<i>P. patula</i>	Pinal de Amoles	202
Maxwell	20-07-05L	<i>P. patula</i>	Pinal de Amoles	208
Maxwell	20-07-05L	<i>P. patula</i>	Pinal de Amoles	211
Maxwell	20-07-05L	<i>P. patula</i>	Pinal de Amoles	212
Maxwell	20-07-05L	<i>P. patula</i>	Pinal de Amoles	214
Maxwell	20-07-05L	<i>P. patula</i>	Pinal de Amoles	218
Maxwell	20-07-05L	<i>P. patula</i>	Pinal de Amoles	219
Maxwell	20-07-05L	<i>P. patula</i>	Pinal de Amoles	222
Maxwell	20-07-05L	<i>P. patula</i>	Conrado Castillo	225
Maxwell	20-07-05L	<i>P. patula</i>	Conrado Castillo	227
Maxwell	20-07-05L	<i>P. patula</i>	Conrado Castillo	228
Maxwell	20-07-05L	<i>P. patula</i>	Conrado Castillo	230
Maxwell	20-07-05L	<i>P. patula</i>	Conrado Castillo	233
Maxwell	20-07-05L	<i>P. patula</i>	Conrado Castillo	237
Maxwell	20-07-05L	<i>P. patula</i>	Conrado Castillo	238
Maxwell	20-07-05L	<i>P. patula</i>	Conrado Castillo	241
Maxwell	20-07-05L	<i>P. patula</i>	Conrado Castillo	243
Maxwell	20-07-07D	<i>P. patula</i>	Zacualltipan	249
Maxwell	20-07-05L	<i>P. patula</i>	Zacualltipan	251
Maxwell	20-07-05L	<i>P. patula</i>	Zacualltipan	252
Maxwell	20-07-05L	<i>P. patula</i>	Zacualltipan	254

<b>Site</b>	<b>Trial</b>	<b>Species</b>	<b>Provenance</b>	<b>Family</b>
Maxwell	20-07-05L	<i>P. patula</i>	Zacualtipan	256
Maxwell	20-07-05L	<i>P. patula</i>	Zacualtipan	257
Maxwell	20-07-05L	<i>P. patula</i>	Zacualtipan	258
Maxwell	20-07-05L	<i>P. patula</i>	Zacualtipan	261
Maxwell	20-07-05L	<i>P. patula</i>	Zacualtipan	262
Maxwell	20-07-06E	<i>P. patula</i>	Llano de las Carmonas	263
Maxwell	20-07-06E	<i>P. patula</i>	Llano de las Carmonas	268
Maxwell	20-07-05L	<i>P. patula</i>	Llano de las Carmonas	270
Maxwell	20-07-05L	<i>P. patula</i>	Llano de las Carmonas	272
Maxwell	20-07-06E	<i>P. patula</i>	Llano de las Carmonas	278
Maxwell	20-07-05L	<i>P. patula</i>	Llano de las Carmonas	280
Maxwell	20-07-05L	<i>P. patula</i>	Llano de las Carmonas	286
Maxwell	20-07-06E	<i>P. patula</i>	Llano de las Carmonas	287
Maxwell	20-07-06E	<i>P. patula</i>	Llano de las Carmonas	288
Maxwell	20-07-05L	<i>P. patula</i>	Tlacotla	289
Maxwell	20-07-05L	<i>P. patula</i>	Tlacotla	290
Maxwell	20-07-06E	<i>P. patula</i>	Tlacotla	292
Maxwell	20-07-05L	<i>P. patula</i>	Tlacotla	293
Maxwell	20-07-05L	<i>P. patula</i>	Tlacotla	295
Maxwell	20-07-06E	<i>P. patula</i>	Tlacotla	297
Maxwell	20-07-06E	<i>P. patula</i>	Tlacotla	301
Maxwell	20-07-06E	<i>P. patula</i>	Tlacotla	305
Maxwell	20-07-05L	<i>P. patula</i>	Tlacotla	309
Maxwell	20-07-02D	<i>P. patula</i>	SA control	999

## Appendix 2

### Analysis of variance table for density traits, provenance analysis .

Source	DF	Type III SS	Mean Square	F Value	Pr > F
<b>Weighted Mean Density (WMD)</b>					
rep	8	0.38036666	0.04754583	38.92	<.0001
prov	12	0.07935791	0.00661316	5.41	<.0001
rep*prov	96	0.16255002	0.00169323	1.39	0.0112
Error	881	1.07635165	0.00122174		
Corrected Total	997	1.73478092			
<b>Mean Earlywood Density (MEWD)</b>					
rep	8	0.08600308	0.01075039	27.29	<.0001
prov	12	0.17099548	0.01424962	36.17	<.0001
rep*prov	96	0.05675009	0.00059115	1.50	0.0021
Error	881	0.34706958	0.00039395		
Corrected Total	997	0.66707273			
<b>Mean Latewood Density (MLWD)</b>					
rep	8	0.03134370	0.00391796	5.64	<.0001
prov	12	0.80697295	0.06724775	96.88	<.0001
rep*prov	96	0.07521781	0.00078352	1.13	0.1977
Error	881	0.61152545	0.00069413		
Corrected Total	997	1.53110290			
<b>Percent Latewood (PLW)</b>					
rep	8	18742.00057	2342.75007	26.21	<.0001
prov	12	7036.39787	586.36649	6.56	<.0001
rep*prov	96	13981.00277	145.63545	1.63	0.0003
Error	881	78759.8686	89.3983		
Corrected Total	997	120228.3238			

## Appendix 2 (cont.)

### Analysis of variance table for density traits, family within provenance analysis.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
<b>Weighted Mean Density (WMD)</b>					
rep	8	0.37972498	0.04746562	42.61	<.0001
prov	12	0.07940510	0.00661709	5.94	<.0001
rep*prov	96	0.16116750	0.00167883	1.51	0.0021
fam(prov)	96	0.20180934	0.00210218	1.89	<.0001
Error	785	0.87454231	0.00111407		
Corrected Total	997	1.73478267			
<b>Mean Earlywood Density (MEWD)</b>					
rep	8	0.08606962	0.01075870	31.03	<.0001
prov	12	0.17112028	0.01426002	41.12	<.0001
rep*prov	96	0.05643766	0.00058789	1.70	<.0001
fam(prov)	96	0.07486464	0.00077984	2.25	<.0001
Error	785	0.27220495	0.00034676		
Corrected Total	997	0.66707273			
<b>Mean Latewood Density (MLWD)</b>					
rep	8	0.03077826	0.00384728	6.03	<.0001
prov	12	0.80738781	0.06728232	105.51	<.0001
rep*prov	96	0.07516119	0.00078293	1.23	0.0783
fam(prov)	96	0.11093560	0.00115558	1.81	<.0001
Error	785	0.50058985	0.00063769		
Corrected Total	997	1.53110290			
<b>Percent Latewood (PLW)</b>					
rep	8	18712.51701	2339.06463	28.41	<.0001
prov	12	7043.66086	586.97174	7.13	<.0001
rep*prov	96	13830.41201	144.06679	1.75	<.0001
fam(prov)	96	14130.34102	147.19105	1.79	<.0001
Error	785	64629.5276	82.3306		
Corrected Total	997	120228.3238			

### Appendix 3

#### Analysis of variance table for growth ring width, provenance analysis.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
<b>Width Growth Ring 2 (GRW2)</b>					
rep	8	74.6669872	9.3333734	1.11	0.3601
prov	12	565.2086485	47.1007207	5.59	<.0001
rep*prov	65	923.3992278	14.2061420	1.69	0.0039
Error	175	1474.381490	8.425037		
Corrected Total	260	2963.982189			
<b>Width Growth Ring 3 (GRW3)</b>					
rep	8	152.490180	19.061273	1.66	0.1040
prov	12	698.329940	58.194162	5.08	<.0001
rep*prov	95	1342.947941	14.136294	1.23	0.0777
Error	608	6963.472901	11.453080		
Corrected Total	723	9212.831427			
<b>Width Growth Ring 4 (GRW4)</b>					
rep	8	63.5115366	7.9389421	0.85	0.5613
prov	12	322.6966284	26.8913857	2.87	0.0007
rep*prov	96	904.3884405	9.4207129	1.01	0.4705
Error	819	7675.779423	9.372136		
Corrected Total	935	8955.230228			
<b>Width Growth Ring 5 (GRW5)</b>					
rep	8	180.338371	22.542296	2.82	0.0044
prov	12	273.762500	22.813542	2.85	0.0007
rep*prov	96	1031.598232	10.745815	1.34	0.0202
Error	858	6868.916139	8.005730		
Corrected Total	974	8358.246340			
<b>Width Growth Ring 6 (GRW6)</b>					
rep	8	343.998698	42.999837	4.61	<.0001
prov	12	836.624877	69.718740	7.48	<.0001
rep*prov	96	1212.235639	12.627455	1.35	0.0172
Error	868	8092.54717	9.32321		
Corrected Total	984	10454.06613			
<b>Width Growth Ring 7 (GRW7)</b>					
rep	8	129.4926460	16.1865808	2.19	0.0261
prov	12	971.3516962	80.9459747	10.96	<.0001
rep*prov	96	819.7525996	8.5390896	1.16	0.1560
Error	868	6411.926618	7.387012		
Corrected Total	984	8324.328674			
<b>Width Growth Ring 8 (GRW8)</b>					
rep	8	134.3090758	16.7886345	2.55	0.0095
prov	12	630.3707795	52.5308983	7.98	<.0001
rep*prov	96	688.2699134	7.1694783	1.09	0.2727
Error	868	5716.427510	6.585746		
Corrected Total	984	7162.039625			
<b>Width Growth Ring 9 (GRW9)</b>					
rep	8	68.6535567	8.5816946	2.28	0.0204
prov	12	600.3640762	50.0303397	13.30	<.0001
rep*prov	96	352.6667914	3.6736124	0.98	0.5464
Error	868	3266.166167	3.762864		
Corrected Total	984	4293.333724			
<b>Width Growth Ring 10 (GRW10)</b>					
rep	8	101.6014552	12.7001819	3.36	0.0008
prov	12	455.0239142	37.9186595	10.04	<.0001
rep*prov	96	501.1836618	5.2206631	1.38	0.0119
Error	868	3279.085344	3.777748		
Corrected Total	984	4338.256186			

### Appendix 3 (cont.)

#### Analysis of variance table for growth ring width, family within provenance analysis.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
<b>Width Growth Ring 2 (GRW2)</b>					
rep	8	48.9748727	6.1218591	0.69	0.7031
prov	12	420.8066599	35.0672217	3.93	<.0001
rep*prov	64	845.8020570	13.2156571	1.48	0.0477
fam(prov)	94	750.9937256	7.9892950	0.89	0.6999
Error	81	723.387764	8.930713		
Corrected Total	260	2963.982189			
<b>Width Growth Ring 3 (GRW3)</b>					
rep	8	173.719130	21.714891	1.92	0.0550
prov	12	682.417372	56.868114	5.03	<.0001
rep*prov	95	1333.537826	14.037240	1.24	0.0755
fam(prov)	96	1172.736630	12.216007	1.08	0.2982
Error	512	5790.736271	11.310032		
Corrected Total	723	9212.831427			
<b>Width Growth Ring 4 (GRW4)</b>					
rep	8	49.561730	6.195216	0.68	0.7126
prov	12	309.346819	25.778902	2.81	0.0009
rep*prov	96	896.331233	9.336784	1.02	0.4345
fam(prov)	96	1054.254104	10.981814	1.20	0.1061
Error	723	6621.525318	9.158403		
Corrected Total	935	8955.230228			
<b>Width Growth Ring 5 (GRW5)</b>					
rep	8	173.989083	21.748635	2.69	0.0064
prov	12	268.705561	22.392130	2.77	0.0011
rep*prov	96	1016.825400	10.591931	1.31	0.0310
fam(prov)	96	710.606455	7.402151	0.92	0.7008
Error	762	6158.309684	8.081771		
Corrected Total	974	8358.246340			
<b>Width Growth Ring 6 (GRW6)</b>					
rep	8	335.716148	41.964518	4.52	<.0001
prov	12	838.989591	69.915799	7.52	<.0001
rep*prov	96	1209.978783	12.603946	1.36	0.0174
fam(prov)	96	918.866142	9.571522	1.03	0.4076
Error	772	7173.68103	9.29233		
Corrected Total	984	10454.06613			
<b>Width Growth Ring 7 (GRW7)</b>					
rep	8	130.9339976	16.3667497	2.28	0.0205
prov	12	969.3379575	80.7781631	11.25	<.0001
rep*prov	96	818.8957947	8.5301645	1.19	0.1170
fam(prov)	96	869.2465266	9.0546513	1.26	0.0547
Error	772	5542.680091	7.179637		
Corrected Total	984	8324.328674			
<b>Width Growth Ring 8 (GRW8)</b>					
rep	8	138.0799924	17.2599990	2.61	0.0081
prov	12	626.9515945	52.2459662	7.90	<.0001
rep*prov	96	688.4295002	7.1711406	1.08	0.2841
fam(prov)	96	608.5672875	6.3392426	0.96	0.5941
Error	772	5107.860223	6.616399		
Corrected Total	984	7162.039625			

**Appendix 3 (cont.)****Width Growth Ring 9 (GRW9)**

rep	8	70.2983776	8.7872972	2.35	0.0167
prov	12	596.9896337	49.7491361	13.32	<.0001
rep*prov	96	348.9021773	3.6343977	0.97	0.5542
fam(prov)	96	383.4829357	3.9946139	1.07	0.3142
Error	772	2882.683232	3.734046		
Corrected Total	984	4293.333724			

**Width Growth Ring 10 (GRW10)**

rep	8	102.1321702	12.7665213	3.47	0.0006
prov	12	453.2817526	37.7734794	10.26	<.0001
rep*prov	96	502.9385869	5.2389436	1.42	0.0072
fam(prov)	96	435.5352468	4.5368255	1.23	0.0753
Error	772	2843.550097	3.683355		
Corrected Total	984	4338.256186			

## Appendix 4

### Analysis of variance table for core region density, provenance analysis.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
<b>Dependent Variable: R2-4</b>					
rep	8	0.19008812	0.02376102	20.41	<.0001
prov	12	0.07865297	0.00655441	5.63	<.0001
rep*prov	96	0.12633891	0.00131603	1.13	0.1952
Error	859	1.00001591	0.00116416		
Corrected Total	975	1.40276731			
<b>Dependent Variable: R5-7</b>					
rep	8	0.28802868	0.03600358	30.99	<.0001
prov	12	0.11079293	0.00923274	7.95	<.0001
rep*prov	96	0.13249167	0.00138012	1.19	0.1154
Error	859	0.99785550	0.00116165		
Corrected Total	975	1.55460180			
<b>Dependent Variable: R8-10</b>					
rep	8	0.69339850	0.08667481	40.32	<.0001
prov	12	0.16158751	0.01346563	6.26	<.0001
rep*prov	96	0.29625744	0.00308602	1.44	0.0057
Error	859	1.84651984	0.00214962		
Corrected Total	975	3.07162974			

### Analysis of variance table for core region density, family within provenance analysis.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
<b>Dependent Variable: R2-4</b>					
rep	8	0.18308121	0.02288515	21.36	<.0001
prov	12	0.07875146	0.00656262	6.13	<.0001
rep*prov	96	0.12562063	0.00130855	1.22	0.0839
fam(prov)	96	0.18269115	0.00190303	1.78	<.0001
Error	763	0.81732476	0.00107120		
Corrected Total	975	1.40276731			
<b>Dependent Variable: R5-7</b>					
rep	8	0.27855343	0.03481918	32.97	<.0001
prov	12	0.11058926	0.00921577	8.73	<.0001
rep*prov	96	0.13402280	0.00139607	1.32	0.0270
fam(prov)	96	0.19198059	0.00199980	1.89	<.0001
Error	763	0.80587492	0.00105619		
Corrected Total	975	1.55460180			
<b>Dependent Variable: R8-10</b>					
rep	8	0.66148828	0.08268604	41.21	<.0001
prov	12	0.16123693	0.01343641	6.70	<.0001
rep*prov	96	0.29994662	0.00312444	1.56	0.0010
fam(prov)	96	0.31543831	0.00328582	1.64	0.0003
Error	763	1.53108153	0.00200666		
Corrected Total	975	3.0716297			

## Appendix 4 (cont.)

### Analysis of variance table for core region density, provenance analysis partitioned into earlywood (E) and latewood (L)

Source	DF	Type III SS	Mean Square	F Value	Pr > F
<b>Dependent Variable: R2-4E</b>					
rep	8	0.05890125	0.00736266	15.09	<.0001
prov	12	0.12675425	0.01056285	21.64	<.0001
rep*prov	96	0.06158097	0.00064147	1.31	0.0287
Error	848	0.41384651	0.00048803		
Corrected Total	964	0.66002836			
<b>Dependent Variable: R5-7E</b>					
rep	8	0.10871204	0.01358901	25.25	<.0001
prov	12	0.26632250	0.02219354	41.24	<.0001
rep*prov	96	0.07218100	0.00075189	1.40	0.0098
Error	848	0.45635645	0.00053816		
Corrected Total	964	0.90880838			
<b>Dependent Variable: R8-10E</b>					
rep	8	0.12556528	0.01569566	31.81	<.0001
prov	12	0.11816319	0.00984693	19.96	<.0001
rep*prov	96	0.07096931	0.00073926	1.50	0.0023
Error	848	0.41837051	0.00049336		
Corrected Total	964	0.74059760			
<b>Dependent Variable: R2-4L</b>					
rep	8	0.02887777	0.00360972	5.79	<.0001
prov	12	0.34022925	0.02835244	45.45	<.0001
rep*prov	96	0.06654944	0.00069322	1.11	0.2291
Error	848	0.52904479	0.00062387		
Corrected Total	964	0.97280957			
<b>Dependent Variable: R5-7L</b>					
rep	8	0.01648496	0.00206062	1.86	0.0637
prov	12	1.02552935	0.08546078	76.98	<.0001
rep*prov	96	0.10445482	0.00108807	0.98	0.5362
Error	848	0.94139086	0.00111013		
Corrected Total	964	2.09710800			
<b>Dependent Variable: R8-10L</b>					
rep	8	0.08313388	0.01039174	5.96	<.0001
prov	12	1.79159632	0.14929969	85.69	<.0001
rep*prov	96	0.16055610	0.00167246	0.96	0.5897
Error	848	1.47752900	0.00174237		
Corrected Total	964	3.53059036			

## Appendix 4 (cont.)

### Analysis of variance table for core region density, family within provenance analysis partitioned into earlywood (E) and latewood (L).

Source	DF	Type III SS	Mean Square	F Value	Pr > F
<b>Dependent Variable: R2-4E</b>					
rep	8	0.05691337	0.00711417	15.86	<.0001
prov	12	0.12536172	0.01044681	23.29	<.0001
rep*prov	96	0.06137446	0.00063932	1.43	0.0070
fam(prov)	96	0.07646791	0.00079654	1.78	<.0001
Error	752	0.33737860	0.00044864		
Corrected Total	964	0.66002836			
<b>Dependent Variable: R5-7E</b>					
rep	8	0.10668127	0.01333516	28.05	<.0001
prov	12	0.26507563	0.02208964	46.46	<.0001
rep*prov	96	0.07297616	0.00076017	1.60	0.0005
fam(prov)	96	0.09879840	0.00102915	2.16	<.0001
Error	752	0.35755805	0.00047548		
Corrected Total	964	0.90880838			
<b>Dependent Variable: R8-10E</b>					
rep	8	0.12126216	0.01515777	33.94	<.0001
prov	12	0.11694610	0.00974551	21.82	<.0001
rep*prov	96	0.07176363	0.00074754	1.67	0.0001
fam(prov)	96	0.08247880	0.00085915	1.92	<.0001
Error	752	0.33589172	0.00044666		
Corrected Total	964	0.74059760			
<b>Dependent Variable: R2-4L</b>					
rep	8	0.02852703	0.00356588	5.89	<.0001
prov	12	0.33679157	0.02806596	46.35	<.0001
rep*prov	96	0.06575227	0.00068492	1.13	0.1962
fam(prov)	96	0.07367964	0.00076750	1.27	0.0513
Error	752	0.45536515	0.00060554		
Corrected Total	964	0.97280957			
<b>Dependent Variable: R5-7L</b>					
rep	8	0.01659496	0.00207437	2.03	0.0409
prov	12	1.02728735	0.08560728	83.64	<.0001
rep*prov	96	0.10316349	0.00107462	1.05	0.3597
fam(prov)	96	0.17170830	0.00178863	1.75	<.0001
Error	752	0.76968256	0.00102351		
Corrected Total	964	2.09710800			
<b>Dependent Variable: R8-10L</b>					
rep	8	0.08642279	0.01080285	6.79	<.0001
prov	12	1.78905978	0.14908832	93.70	<.0001
rep*prov	96	0.16134118	0.00168064	1.06	0.3450
fam(prov)	96	0.28100118	0.00292710	1.84	<.0001
Error	752	1.19652783	0.00159113		
Corrected Total	964	3.53059036			

## Appendix 5

### Analysis of variance table for individual ring tracheid length, provenance analysis.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
<b>Ring 2</b>					
rep	8	10.34801874	1.29350234	57.42	<.0001
prov	12	1.37651601	0.11470967	5.09	<.0001
rep*prov	96	6.04224610	0.06294006	2.79	<.0001
Error	777	17.50493875	0.02252888		
Corrected Total	893	36.45746653			
<b>Ring 4</b>					
rep	8	5.62639788	0.70329973	18.81	<.0001
prov	12	1.90511326	0.15875944	4.25	<.0001
rep*prov	96	6.32767240	0.06591325	1.76	<.0001
Error	877	32.79479326	0.03739429		
Corrected Total	993	46.94930587			
<b>Ring 6</b>					
rep	8	9.02406498	1.12800812	17.39	<.0001
prov	12	1.64222916	0.13685243	2.11	0.0143
rep*prov	96	13.63544777	0.14203591	2.19	<.0001
Error	879	57.00746780	0.06485491		
Corrected Total	995	81.81875147			
<b>Ring 8</b>					
rep	8	11.87284638	1.48410580	22.80	<.0001
prov	12	2.35930085	0.19660840	3.02	0.0004
rep*prov	96	11.60147843	0.12084873	1.86	<.0001
Error	879	57.21325021	0.06508902		
Corrected Total	995	84.27555162			
<b>Ring 10</b>					
rep	8	67.02534591	8.37816824	123.11	<.0001
prov	12	2.87871710	0.23989309	3.53	<.0001
rep*prov	96	9.74939365	0.10155618	1.49	0.0024
Error	876	59.6149217	0.0680536		
Corrected Total	992	145.3815672			

## Appendix 5 (cont.)

### Analysis of variance table for mean age tracheid length, provenance analysis.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
<b>Age 2</b>					
rep	8	10.34801874	1.29350234	57.42	<.0001
prov	12	1.37651601	0.11470967	5.09	<.0001
rep*prov	96	6.04224610	0.06294006	2.79	<.0001
Error	777	17.50493875	0.02252888		
Corrected Total	893	36.45746653			
<b>Age 4</b>					
rep	8	7.77470030	0.97183754	48.71	<.0001
prov	12	1.53819574	0.12818298	6.42	<.0001
rep*prov	96	4.04668028	0.04215292	2.11	<.0001
Error	777	15.50255262	0.01995181		
Corrected Total	893	29.40990991			
<b>Age 6</b>					
rep	8	7.62978703	0.95372338	43.82	<.0001
prov	12	1.27745891	0.10645491	4.89	<.0001
rep*prov	96	4.30961174	0.04489179	2.06	<.0001
Error	776	16.88872996	0.02176383		
Corrected Total	892	30.34673281			
<b>Age 8</b>					
rep	8	5.70048659	0.71256082	33.29	<.0001
prov	12	1.26662561	0.10555213	4.93	<.0001
rep*prov	96	4.25304321	0.04430253	2.07	<.0001
Error	776	16.60866790	0.02140292		
Corrected Total	892	27.97575162			
<b>Age 10</b>					
rep	8	2.48197262	0.31024658	15.74	<.0001
prov	12	1.26993148	0.10582762	5.37	<.0001
rep*prov	96	3.82744620	0.03986923	2.02	<.0001
Error	774	15.25484395	0.01970910		
Corrected Total	890	22.93414219			

## Appendix 5 (cont.)

### Analysis of variance table for individual ring tracheid length, family within provenance analysis.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
<b>Ring 2</b>					
rep	8	10.06122281	1.25765285	57.11	<.0001
prov	12	1.33783904	0.11148659	5.06	<.0001
rep*prov	96	5.96025591	0.06208600	2.82	<.0001
fam(prov)	96	2.50778586	0.02612277	1.19	0.1212
Error	681	14.99715289	0.02202225		
Corrected Total	893	36.45746653			
<b>Ring 4</b>					
rep	8	5.62705926	0.70338241	19.22	<.0001
prov	12	1.90433318	0.15869443	4.34	<.0001
rep*prov	96	6.27347420	0.06534869	1.79	<.0001
fam(prov)	96	4.20595881	0.04381207	1.20	0.1072
Error	781	28.58883445	0.03660542		
Corrected Total	993	46.94930587			
<b>Ring 6</b>					
rep	8	9.02723516	1.12840440	18.22	<.0001
prov	12	1.64075477	0.13672956	2.21	0.0100
rep*prov	96	13.64960086	0.14218334	2.30	<.0001
fam(prov)	96	8.51327912	0.08867999	1.43	0.0063
Error	783	48.49418868	0.06193383		
Corrected Total	995	81.81875147			
<b>Ring 8</b>					
rep	8	11.82664707	1.47833088	22.53	<.0001
prov	12	2.36151392	0.19679283	3.00	0.0004
rep*prov	96	11.60280508	0.12086255	1.84	<.0001
fam(prov)	96	5.83040868	0.06073342	0.93	0.6776
Error	783	51.38284152	0.06562304		
Corrected Total	995	84.27555162			
<b>Ring 10</b>					
rep	8	66.37827161	8.29728395	126.19	<.0001
prov	12	2.85266823	0.23772235	3.62	<.0001
rep*prov	96	9.79319244	0.10201242	1.55	0.0010
fam(prov)	96	8.32645019	0.08673386	1.32	0.0278
Error	780	51.2884715	0.0657545		
Corrected Total	992	145.3815672			

## Appendix 5 (cont.)

### Analysis of variance table for mean age tracheid length, family within provenance analysis.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
<b>Age 2</b>					
rep	8	10.06122281	1.25765285	57.11	<.0001
prov	12	1.33783904	0.11148659	5.06	<.0001
rep*prov	96	5.96025591	0.06208600	2.82	<.0001
fam(prov)	96	2.50778586	0.02612277	1.19	0.1212
Error	681	14.99715289	0.02202225		
Corrected Total	893	36.45746653			
<b>Age 4</b>					
rep	8	7.54087186	0.94260898	47.71	<.0001
prov	12	1.48851280	0.12404273	6.28	<.0001
rep*prov	96	3.97979242	0.04145617	2.10	<.0001
fam(prov)	96	2.04672062	0.02132001	1.08	0.2959
Error	681	13.45583200	0.01975893		
Corrected Total	893	29.40990991			
<b>Age 6</b>					
rep	8	7.35710898	0.91963862	43.34	<.0001
prov	12	1.23246563	0.10270547	4.84	<.0001
rep*prov	96	4.19028761	0.04364883	2.06	<.0001
fam(prov)	96	2.45858399	0.02561025	1.21	0.0993
Error	680	14.43014597	0.02122080		
Corrected Total	892	30.34673281			
<b>Age 8</b>					
rep	8	5.47969543	0.68496193	32.50	<.0001
prov	12	1.25821756	0.10485146	4.98	<.0001
rep*prov	96	4.12068928	0.04292385	2.04	<.0001
fam(prov)	96	2.27914275	0.02374107	1.13	0.2053
Error	680	14.32952515	0.02107283		
Corrected Total	892	27.97575162			
<b>Age 10</b>					
rep	8	2.42929985	0.30366248	15.71	<.0001
prov	12	1.29895519	0.10824627	5.60	<.0001
rep*prov	96	3.71207377	0.03866744	2.00	<.0001
fam(prov)	96	2.14821329	0.02237722	1.16	0.1577
Error	678	13.10663066	0.01933131		
Corrected Total	890	22.93414219			

## Appendix 6

### Analysis of variance table for tracheid cross-sectional properties, provenance analysis.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
<b>Dependent Variable: RD</b>					
rep	8	271.861717	33.982715	4.56	<.0001
prov	12	2258.706896	188.225575	25.27	<.0001
rep*prov	96	631.628795	6.579467	0.88	0.7771
Error	876	6526.108715	7.449896		
Corrected Total	992	9724.737137			
<b>Dependent Variable: TD</b>					
rep	8	343.2378686	42.9047336	14.03	<.0001
prov	12	763.7345774	63.6445481	20.81	<.0001
rep*prov	96	300.0697646	3.1257267	1.02	0.4274
Error	876	2679.631061	3.058940		
Corrected Total	992	4090.690523			
<b>Dependent Variable: LD</b>					
rep	8	300.384051	37.548006	10.39	<.0001
prov	12	1322.610838	110.217570	30.51	<.0001
rep*prov	96	404.480852	4.213342	1.17	0.1416
Error	876	3164.306175	3.612222		
Corrected Total	992	5244.316547			
<b>Dependent Variable: WA</b>					
rep	8	997245.3187	124655.6648	34.97	<.0001
prov	12	313189.7158	26099.1430	7.32	<.0001
rep*prov	96	855032.9740	8906.5935	2.50	<.0001
Error	876	3123044.035	3565.119		
Corrected Total	992	5357985.063			
<b>Dependent Variable: WT</b>					
rep	8	101.9549277	12.7443660	50.15	<.0001
prov	12	7.0574128	0.5881177	2.31	0.0065
rep*prov	96	80.5530402	0.8390942	3.30	<.0001
Error	876	222.5963850	0.2541055		
Corrected Total	992	421.8042381			

## Appendix 6 (cont.)

### Analysis of variance table for derived tracheid cross-sectional properties, provenance analysis.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
<b>Dependent Variable: TArea</b>					
rep	8	16062229.08	2007778.64	8.09	<.0001
prov	12	77082571.07	6423547.59	25.89	<.0001
rep*prov	96	22097572.78	230183.05	0.93	0.6725
Error	876	217329788.6	248093.4		
Corrected Total	992	333449147.4			
<b>Dependent Variable: NoTrach</b>					
rep	8	38234.0239	4779.2530	8.10	<.0001
prov	12	170866.3518	14238.8627	24.13	<.0001
rep*prov	96	51183.0425	533.1567	0.90	0.7311
Error	876	516852.5580	590.0143		
Corrected Total	992	779504.7470			
<b>Dependent Variable: PCell</b>					
rep	8	5383.283370	672.910421	44.71	<.0001
prov	12	1823.297064	151.941422	10.10	<.0001
rep*prov	96	4341.270498	45.221568	3.00	<.0001
Error	876	13183.34336	15.04948		
Corrected Total	992	25316.22428			
<b>Dependent Variable: RR</b>					
rep	8	0.85696947	0.10712118	38.70	<.0001
prov	12	0.40830918	0.03402576	12.29	<.0001
rep*prov	96	0.77063042	0.00802740	2.90	<.0001
Error	876	2.42478003	0.00276801		
Corrected Total	992	4.56360806			

## Appendix 6 (cont.)

### Analysis of variance table for derived (SilviScan®) tracheid cross-sectional properties, provenance analysis.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
<b>Dependent Variable: CS</b>					
rep	8	939141.307	117392.663	21.77	<.0001
prov	12	1655040.466	137920.039	25.58	<.0001
rep*prov	96	570198.622	5939.569	1.10	0.2470
Error	876	4723903.406	5392.584		
Corrected Total	992	7940480.608			
<b>Dependent Variable: WTS</b>					
rep	8	15.21460732	1.90182591	35.90	<.0001
prov	12	10.08139354	0.84011613	15.86	<.0001
rep*prov	96	6.36403830	0.06629207	1.25	0.0595
Error	876	46.40628876	0.05297522		
Corrected Total	992	79.36862840			
<b>Dependent Variable: SS</b>					
rep	8	123912.7793	15489.0974	35.97	<.0001
prov	12	75853.7479	6321.1457	14.68	<.0001
rep*prov	96	54016.1960	562.6687	1.31	0.0312
Error	876	377178.9901	430.5696		
Corrected Total	992	643113.4988			
<b>Dependent Variable: PM</b>					
rep	8	4380.72775	547.59097	7.74	<.0001
prov	12	21924.68698	1827.05725	25.83	<.0001
rep*prov	96	6216.25377	64.75264	0.92	0.7033
Error	876	61971.09271	70.74326		
Corrected Total	992	94766.09749			

## Appendix 6 (cont.)

### Analysis of variance table for tracheid cross-sectional properties, family within provenance analysis.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
<b>Dependent Variable: RD</b>					
rep	8	272.855224	34.106903	5.49	<.0001
prov	12	2251.907023	187.658919	30.22	<.0001
rep*prov	96	632.953972	6.593271	1.06	0.3317
fam(prov)	96	1683.117420	17.532473	2.82	<.0001
Error	780	4842.991295	6.208963		
Corrected Total	992	9724.737137			
<b>Dependent Variable: TD</b>					
rep	8	344.2088453	43.0261057	15.39	<.0001
prov	12	762.5785176	63.5482098	22.74	<.0001
rep*prov	96	300.8495596	3.1338496	1.12	0.2123
fam(prov)	96	499.5454458	5.2035984	1.86	<.0001
Error	780	2180.085615	2.794982		
Corrected Total	992	4090.690523			
<b>Dependent Variable: LD</b>					
rep	8	296.488636	37.061079	11.53	<.0001
prov	12	1320.169788	110.014149	34.21	<.0001
rep*prov	96	399.615165	4.162658	1.29	0.0372
fam(prov)	96	656.239923	6.835833	2.13	<.0001
Error	780	2508.066252	3.215470		
Corrected Total	992	5244.316547			
<b>Dependent Variable: WA</b>					
rep	8	1002594.767	125324.346	37.66	<.0001
prov	12	312340.354	26028.363	7.82	<.0001
rep*prov	96	859880.660	8957.090	2.69	<.0001
fam(prov)	96	527084.617	5490.465	1.65	0.0002
Error	780	2595959.417	3328.153		
Corrected Total	992	5357985.063			
<b>Dependent Variable: WT</b>					
rep	8	102.0717759	12.7589720	50.57	<.0001
prov	12	7.0500432	0.5875036	2.33	0.0063
rep*prov	96	80.5832248	0.8394086	3.33	<.0001
fam(prov)	96	25.8004839	0.2687550	1.07	0.3243
Error	780	196.7959011	0.2523024		
Corrected Total	992				

## Appendix 6 (cont.)

### Analysis of variance table for derived tracheid cross-sectional properties, family within provenance analysis.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
<b>Dependent Variable: TArea</b>					
rep	8	16107918.27	2013489.78	9.63	<.0001
prov	11	74913334.94	6810303.18	32.58	<.0001
rep*prov	88	20353222.30	231286.62	1.11	0.2463
fam(prov)	96	51668585.43	538214.43	2.58	<.0001
Error	764	159687611.3	209015.2		
Corrected Total	967	322866145.0			
<b>Dependent Variable: NoTrach</b>					
rep	8	38774.5317	4846.8165	9.52	<.0001
prov	11	165994.0711	15090.3701	29.63	<.0001
rep*prov	88	47837.1785	543.6043	1.07	0.3246
fam(prov)	96	116669.8552	1215.3110	2.39	<.0001
Error	764	389101.4993	509.2952		
Corrected Total	967	758589.9466			
<b>Dependent Variable: PCell</b>					
rep	8	5711.162942	713.895368	47.91	<.0001
prov	11	1761.366714	160.124247	10.75	<.0001
rep*prov	88	4261.548040	48.426682	3.25	<.0001
fam(prov)	96	1594.153920	16.605770	1.11	0.2247
Error	764	11383.92230	14.90042		
Corrected Total	967	24825.22420			
<b>Dependent Variable: RR</b>					
rep	8	0.92240171	0.11530021	41.72	<.0001
prov	11	0.39179557	0.03561778	12.89	<.0001
rep*prov	88	0.76043185	0.00864127	3.13	<.0001
fam(prov)	96	0.27968149	0.00291335	1.05	0.3497
Error	764	2.11144470	0.00276367		
Corrected Total	967	4.48341312			

## Appendix 6 (cont.)

### Analysis of variance table for (SilviScan®) derived tracheid cross-sectional properties, family within provenance analysis.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
<b>Dependent Variable: CS</b>					
rep	8	947787.805	118473.476	25.76	<.0001
prov	12	1647289.363	137274.114	29.84	<.0001
rep*prov	96	579281.202	6034.179	1.31	0.0303
fam(prov)	96	1136056.402	11833.921	2.57	<.0001
Error	780	3587847.004	4599.804		
Corrected Total	992	7940480.608			
<b>Dependent Variable: WTS</b>					
rep	8	15.29169070	1.91146134	40.35	<.0001
prov	12	10.02205414	0.83517118	17.63	<.0001
rep*prov	96	6.42058270	0.06688107	1.41	0.0083
fam(prov)	96	9.45498788	0.09848946	2.08	<.0001
Error	780	36.95130088	0.04737346		
Corrected Total	992	79.36862840			
<b>Dependent Variable: SS</b>					
rep	8	124510.7114	15563.8389	40.19	<.0001
prov	12	75373.2441	6281.1037	16.22	<.0001
rep*prov	96	54407.4303	566.7441	1.46	0.0040
fam(prov)	96	75104.4950	782.3385	2.02	<.0001
Error	780	302074.4951	387.2750		
Corrected Total	992	643113.4988			
<b>Dependent Variable: PM</b>					
rep	8	4401.82221	550.22778	9.09	<.0001
prov	12	21869.06720	1822.42227	30.11	<.0001
rep*prov	96	6232.15292	64.91826	1.07	0.3076
fam(prov)	96	14768.17902	153.83520	2.54	<.0001
Error	780	47202.91370	60.51656		
Corrected Total	992	94766.09749			