

ABSTRACT

KANZLER, ARNULF. Genotype x Environment Interaction in *Pinus patula* and its Implications in South Africa. (Under the direction of Gary R. Hodge).

The Genotype x environment interaction was examined using 81 provenance and / or progeny tests of *Pinus patula* over 54 sites in Southern Africa (South Africa and Swaziland). Type B genetic correlation estimates were calculated for all possible pairs of tests amongst these trials. The mean Type B genetic correlation for all tests across all sites was 0.69. The difference between the imported Mexican provenance material and a range of South African genetically improved populations was minimal with estimates of 0.68 and 0.70, respectively. Standardization of the data had a small but significant effect on the estimates of genotype x environment interaction with increasing significance as growth differences amongst tests increased. The proportion of interactive genotypes was examined using the joint regression method, and varied markedly between populations. Amongst the imported Mexican material, the most interactive populations were found to be those originating from the northern part of the distribution of *P. patula* in Mexico. The proportion of interactive genotypes varied from 9 – 40% amongst the Mexican material and 10 – 16% for the South African families. Interacting environments were not restricted to a small number of sites and moderate levels of genotype x environment interaction were found across most sites. A range of climatic factors was examined in an attempt to define regions of predictable, minimal genotype x environment interaction. Some variables related to

the spring rainfall and winter potential evaporation were identified and utilized in provisional models that were able to differentiate a difference in Type B genetic correlation estimates of 0.11. Small predicted genetic gains of between 0.5 – 1.5 % were estimated when utilizing the benefits of regionalization as proposed in these models. The breeding strategy and testing procedures are discussed in the context of *P. patula* within the region.

**Genotype x Environment Interaction in *Pinus patula* and
its Implications in South Africa**

by

Arnulf Kanzler

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

DEPARTMENT OF FORESTRY
Raleigh, NC
2002

Approved by

Gary R. Hodge,
Chair of Advisory Committee

William S. Dvorak,
Member of the Advisory Committee

H.Lee Allen,
Member of the Advisory Committee

Bailian Li,
Member of the Advisory Committee

**This dissertation is dedicated to my three 'girls'
Patricia, Savanna and Anja
and to my parents, Richard & Ilse Kanzler**

BIOGRAPHY

Arnulf Kanzler was born on 24 March, 1961 in Kaduna, Nigeria. He was educated at Treverton, Mooi River and Alexander High School in Pietermaritzburg, South Africa, matriculating in 1978. He then proceeded to the University of Natal (Pietermaritzburg) reading for a BSc degree and graduating in 1981 with Botany and Zoology as major subjects. He spent a year working in Germany before returning to the University of Natal, South Africa, to complete an Honours degree in Botany in 1983, followed by a Higher Education Diploma in 1984.

He then served his 2 years compulsory military service in the South African Defence Force. On his discharge, he taught Biology and Science at Carter High School in Pietermaritzburg, for the next 4 years. In 1991 he joined Sappi Forest Research and worked as a Research Officer in the Pine Breeding Program. During this time he completed several Genetics, Mathematics and Biometry courses through the University of Natal, Pietermaritzburg. In 1994 he took up a contract with Usutu Pulp Company, Swaziland and worked there as a Tree Breeder until July 1998.

During 1998 he was awarded a CAMCORE stipend and the opportunity to read for a Masters with the Department of Forestry at North Carolina State University in Raleigh, USA, commencing in August of that year. During this period of study, he was able to upgrade his Masters to a Ph.D. in Forestry. He completed most of his course work while in Raleigh and returned to South Africa in January 2000 to take up his current position. He is the Pine Program Leader for Softwood Breeding in Sappi Forest Research, South Africa.

ACKNOWLEDGEMENTS

I would like to express my sincere appreciation to my committee members, Dr. William Dvorak, Dr. H. Lee Allen and Dr Bailian Li. Special thanks go to Dr Gary Hodge (Chairman) who provided invaluable guidance and direction, and has, along with his family - Terry, Daniel, Megan and Rebecca - been most hospitable during my stay in the United States of America. My thanks also go to Mark and Tina Rose for their support and friendship in the final weeks here in Raleigh.

There are many others whom I'd like to thank. Firstly, to my parents who have encouraged me over the years. To Dr Andrew Morris, who has always strongly supported my endeavours and whose vision provided the impetus for this PhD. To the staff of Sappi and Camcore, I am most grateful for their companionship, in particular, Giovanni Sale and William Woodbridge for help with the maps and figures, Rob Pallett for helping with the Silviculture aspects and Alane Basco-Rodilas for helping with the administrative side of things.

The following organizations and individuals have also helped with this thesis: Mondi, Safcol, ICFR and the CSIR for providing data, access to sites and other information – special thanks to Eric Kietzka (Mondi), Cecelia Bester (Safcol) and Richard Kunz (ICFR). Some of the data utilized was also obtained from the CSIR.

I would like to thank my company, Sappi, to whom I am deeply indebted for their financial support, without which, this would not have been possible. I would also like to sincerely thank Camcore for their financial support and, in particular, to Dr William Dvorak for his encouragement through the years.

Finally, I would like to thank my wife, Patricia, and my two daughters, Savanna and Anja, for their patience, love and understanding. This is best summed up by this note written by my seven-year old daughter, in which she encouraged me to go and complete my PhD in no uncertain terms:

“ dear papa
ples finish your work I am wiling to play with you
lots love savanna”

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CHAPTER 1 – INTRODUCTION, OBJECTIVES, AND THESIS OUTLINE

1.1 An introduction to forestry in South Africa

1.1.1 South Africa, despite being generally regarded as a region with an arid climate, supports a successful and vibrant forestry industry. The commercial timber plantation area at 30 June 1998 was just over 1.5 million hectares which represents around 1.2% of the total area of the country (Department of Water Affairs and Forestry, 1998). The total roundwood production from this landbase is estimated at 16.5 million m³ for 1998 and represents a total value of timber product sales of R9144 million per annum. The forest industry contributed around 7% of the country's agricultural output during the same year (Department of Water Affairs and Forestry, 1998). These timber products support secondary industries such as sawtimber, pulp and paper and mining timber, amongst others, which contributed R8.6 billion, or 2% of GDP, to the South African economy in 1994 (Versveld et al., 1994).

1.1.2 The Softwood plantation area represents around 50% of the total afforested land (794451ha) and is utilized roughly equally for both sawlog and pulpwood production. As of 1998, *Pinus patula* was planted on 375883ha (Department of Water Affairs and Forestry, 1998), which is just under half of the total area planted to softwoods. All commercial plantings of this species are restricted to the summer rainfall areas representing the forestry regions stretching from the Eastern Cape in a narrow band along the eastern escarpment, through KwaZulu-Natal, Mpumalanga and into the Northern Province.

1.1.3 Recent investments, particularly in the pulp and paper industries, suggest that further growth in demand for timber is likely to continue to increase (Molony, 1999). To meet this demand forestry companies will need to increase timber output. This may be done either by increasing the amount of timber attainable from the existing landbase, or through expansion of the plantation area (Kimmins, 1994). Southern Africa as a whole, is generally a dry area with only limited additional area having the potential for further afforestation (Versveld et al., 1994). The actual area available is likely to be even less due to political, environmental and economic constraints. This clearly suggests that increasing the productivity of areas currently under plantation management is a pragmatic and viable option. This demands more intensive and well managed silviculture.

1.2 Background and rationale for current research

1.2.1 Intensive silviculture involves optimizing and manipulating the available resources, through the correct choice of genotype, protecting them from damaging agents and by enhancing

the environment above and below ground (Schonau, 1989). Genotype-site matching includes choosing the correct species as well as identifying the best genotypes within species for a specific environment. This represents a major aspect of realizing gains from plantation forestry and the correct choice of species and seed source represents a vital first step in this process (Zobel and Talbert, 1984). In South Africa, work focused initially on identifying the correct species for the correct site and this has been well documented (Poynton, 1957), (Poynton, 1966), (Schonau and Fitzpatrick, 1981), (Schonau and Grey, 1987), (Schutz, 1994). More specifically, this work included, recent research in identifying the specific site requirements for *P. patula* continues today (Evans, 1974), (Grey, 1979), (Schutz, 1990), (Louw, 1995) and (Pallett, 1999).

1.2.2 Genetic improvement with *P. patula* was initiated, both in Zimbabwe (Mullin, 1990) and South Africa (Poynton, 1979), in the late 1950's, with some organizations now starting the third cycle of selection and breeding. Consideration of the future operational environment of forestry in Southern Africa suggests that deployment will be aimed at maximizing both gains from the breeding programs and from a silvicultural management perspective. Several organizations are already deploying open pollinated families of *P. patula* with substantial associated gains being reported (Stanger, 1998). Furthermore, commercial clonal forestry is already a reality with *Eucalytus grandis* and hybrids in South Africa (Denison and Kietzka, 1993) and research into clonal propagation and deployment of *P. patula* is at an advanced stage (Jones et al., 2000). The silvicultural management of forestland is also intensifying resulting in more site-specific silviculture. The latter changes may lead to long term changes in resource availability and thus a changed environment leading to an improvement in site index (Allen et al., 1990). These changes in the environment, achieved by implementing more intensive silviculture, if associated with demonstrable GxE, can be utilized to exploit and further enhance gains in productivity. This has been suggested for the case of *P. taeda* in the S.E. USA (McKeand et al., 1997). Are the genotypes we select in genetic tests the best material when planted out on sites managed quite differently?

1.2.3 Furthermore, *P. patula* is deployed in commercial plantations over a large range of sites and is the most widely distributed softwood planted operationally in the summer rainfall regions (Department of Water Affairs and Forestry, 1998). The latitudinal range of the species encompasses an area from 22°58'S to 30°35'S and includes areas with large differences in site qualities, altitudes, temperature regimes and rainfall conditions. These large site differences suggest that GxE may be present, and indeed, indications from several previous studies support this assertion (Denison, 1973), (Falkenhagen, 1979), (Barnes et al., 1992), (Snedden and Verry, 1999), the only exception being a study of two sites in Mpumalanga Province (Van Wyk and Falkenhagen, 1984).

1.2.4 The discussion above suggests that a comprehensive, national study of genotype by environment interaction (GxE) should be considered and indeed may become even more important in future, with the moves to capitalize on greater productivity gains from improved genetic material and more intensively managed sites. Yet to date no such study has been initiated to look at the question of GxE on a regional basis. There are several reasons for this. Generally, genetic and site effects are much stronger than the genetic-site interaction (Wright, 1973). Thus even if a significant GxE interaction effect is present, significant progress can be made by simply identifying and selecting for good general performers. In addition, even if the GxE variance is deemed large enough to have a detrimental effect on progress with genetic gain, it is in the majority of cases very difficult to define the environmental variables causing the interaction. For genotypes to be matched to environments, those environments must be well defined and repeatable (Matheson and Cotterill, 1990). This requires a large number of sites representing, or sampling a range of environments. In other words, it is difficult and expensive to manage GxE and it is therefore not surprising that its potential to increase production has been ignored by many breeders (Barnes et al., 1984). However, it has been stated that 'perhaps the most serious error in forest management is to ignore genotype x environment' (Zobel and Talbert, 1984). It is thus the intention of the author to consider this aspect within *P. patula*.

1.2.5 A range of material is available for this study. This includes a series of CAMCORE progeny/provenance trials as well as a set of provenance trials collected by FAO representing a structured sample of the full range of the native population of the species in Mexico. In addition, a comprehensive series of progeny trials representing a sample of genotypes from the local land race, at various levels of genetic improvement, and selected in different regions of the country, will also be analyzed. All of the above tests provide a unique opportunity to address the question, and also allow for a degree of co-operation amongst all the breeding programs in the sub-region. Within the region, three organizations are CAMCORE members and have been breeding actively with *P. patula*. These organizations own or manage land throughout the entire region where *P. patula* is planted, stretching from Louis Trichardt in the North (23°S), through Swaziland and South Africa, as far south as 31°S. More details of the nature of these tests are provided in the following chapters.

1.3 Research objectives

1.3.1 To estimate the magnitude and extent of genotype x environment interaction within *Pinus patula* in the Southern Africa region.

1.3.2 To identify the patterns and statistical causes that contribute to the GxE variance present. Is the GxE due to actual rank changes or related to differences in the level of responses amongst genotypes? To what extent can taking cognizance of the heterogeneity of variance amongst different sites eliminate GxE? What proportion of the total genotypes and /or environments are responsible for the GxE?

1.3.3 To construct a model for the rational deployment and breeding of *Pinus patula* in the region. To what extent are these interactions linked to key environmental variables? Is it possible to divide the region up into areas of 'minimal' interaction?

1.3.4 To estimate the cost/benefit of breeding/deployment of *P. patula* based on various regionalization scenarios.

1.3.5 To develop a proposal for a future GxE trial focused on answering many of these questions in greater detail.

1.4 Thesis structure

1.4.1 *Chapter 1 – Introduction* – Introduction, setting the scene, declaring the objectives and defining the scope of the project.

1.4.2 *Chapter 2 – Literature review* - A review of *P. patula* in the context of the environment under which it grows, both in its home range in Mexico and as introduced species in Southern Africa. The review also includes a look at some of the previous work on genotype x environment interaction (GxE) with special reference to tree breeding and considers some of the statistical methodology associated with this work. The growth and silviculture of the species is reviewed in attempt to gain an understanding of the growth and physiology of the species. Finally, the issue of the practical utilization of GxE is discussed and previous studies considered.

1.4.3 *Chapter 3 – Genotype X Environment Interaction in a Series of Provenance/Progeny trials of Pinus patula in South Africa* – The majority of the CAMCORE tests were analyzed using the Type B genetic correlation methods. Details of the trials, sites and population structure are outlined and some attempt at identifying predictable GxE is made. This was produced as a paper for a conference presented in Durban, South Africa. In: Proceedings of a conference on Forest Genetics for the Next Millennium, IUFRO Working Party 2.08.01. 8-13 October, 2000, Durban, South Africa. pp. 151-157

- 1.4.4 *Chapter 4 - An assessment of the extent and amount of GxE in Southern Africa using the Type B genetic correlation method* - All the available progeny and provenance trials, including those utilized in chapter 3 are assembled and analyzed. This information is used to estimate the magnitude and extent of GxE present within the sub-region. The Type B genetic correlations allow the grouping of tests into regions of similar and less similar environments.
- 1.4.5 *Chapter 5 – Identification of the patterns and statistical causes that contribute to the GxE variance* - Selected subsets of the trials are examined in more detail to determine the nature of the interactions. The tests are re-analyzed using standardized data to determine the impact of heterogeneous variances on the GxE. The joint regression method is utilized to try to understand the reaction of the individual genotypes to the environment and to quantify the extent of the genotypes that may be classified as interactive. The impact of the sites themselves is critically examined to determine if the interaction is restricted to only a small number of sites. Finally, several populations of *P. patula* are compared over similar sites to determine the effect of populations on the size and type of interactions.
- 1.4.6 *Chapter 6 - Determination of the key environmental variables that contribute to the GxE and development of breeding and deployment models for P. patula.* – The effect of a range of environmental variables on the growth of *P. patula* is examined. A site factor study is utilized to identify key factors in the environment. These are then assessed in terms of their impact on the GxE in an attempt to identify ‘regions of minimal interaction’ using the Type B genetic correlations calculated previously. GxE models for the species and sub-region are proposed based on various regionalisation options. The models are discussed in the context of the biology and ecology of the species.
- 1.4.7 *Chapter 7 – Conclusions and evaluation of the practical application of GxE* – The results of the previous chapters is synthesized and discussed holistically. Some calculations of the potential genetic gain are made and the practical applications of the results of the research are discussed.

CHAPTER 2 – LITERATURE REVIEW

Chapter Summary

- 2.1 *A review of Genotype x Environment Interaction (GxE)*
- 2.2 *Techniques for evaluating the Genotype x Environment interaction*
- 2.3 *The utilization of GxE for maximum genetic gain*
- 2.4 *An introduction to Pinus patula*
- 2.5 *Site, silviculture and growth of P. patula*
- 2.6 *Evidence for GxE with P. patula*

2.1 A review of Genotype x Environment interaction

2.1.1 Genotype x environment interaction results when the relative performance of genotypes differ when grown in different environments (Zobel and Talbert, 1984). This can be expressed symbolically in the following simple model :-

$P = G + E + GE$ (where P = phenotypic value, G = the genetic effect, E = an environmental effect, and GE = an effect due to genotype x environment interaction).

The dilemma for breeders is that, on the one hand, genotype x environment interaction (GxE) tends to hamper progress by necessitating larger replication in space; while, on the other hand, a strong interaction offers the opportunity to increase gains by developing specific genotypes which will do well in specific environments (Squillace, 1969).

2.1.2 The above suggests that there are two general approaches which can be utilized in dealing with GxE (St.Clair and Kleinschmidt, 1986), (Raymond and Namkonng, 1990). The first way is to characterize the area and then choose the best genotype for each site, this approach maximizes the yield over the total range of planting sites. The second option is to find stable genotypes that perform well over all environments, this will 'guarantee' a minimum yield at each site. Both of these methods have been utilized and will be briefly discussed below. A large amount of research on GxE on forest trees has been summarized in several excellent general reviews (Squillace, 1970), (Shelbourne, 1972), (Shelbourne and Campbell, 1976), (Bridgewater and Stonecypher, 1978), (Skroppa, 1984), (Barnes et al., 1984), (Barnes, 1984), (Matheson and Cotterill, 1990). Some reviews have focused specifically on provenance x environment interaction (Burley and Kemp, 1972), (Wright, 1973), (Matheson and Raymond, 1984) and (Matheson and Raymond, 1986) while 2 have focused on GxE in a South African context (Falkenhagen, 1985), (Van Wyk and Falkenhagen, 1984). Still other good reviews have look at the impact of GxE in other agricultural crops or focused on the statistical aspects (Comstock and Moll, 1963), (Freeman, 1973), (Hill, 1975), (Kang, 1990), (Kang and Gauch, 1996). It is the intention of the author to highlight some of the important studies, summarize key findings and then focus on the work which has relevance to the approach proposed in this study.

2.1.3 It is necessary to define and consider the scope of both the word environment and the genotype, as well as the interaction of the two. The environment can be defined as any factor or combination of factors that can influence the trait of interest (Skroppa, 1984). More specifically it can be classified as "predictable" or "unpredictable" (Shelbourne, 1972). Artificial or silvicultural factors that are under the control of management can be regarded as "predictable" variation.

Other “natural” variation in the environment such as rainfall, latitude, altitude or any other factor that could be measured and related to tree growth would fall in the category of “predictable” variation. “Unpredictable” variation could be any changes that happen over time, either annually or monthly, or any interactions of the above factors that are not immediately apparent to the researcher. Genotype can be defined as ‘any genetic entity with a degree of repeatability’ (Wright, 1976). This encompasses species, provenance, family and individual. In this work the author is primarily interested in GxE at the provenance and family level.

2.1.4 The interaction of genotype and environment (GxE) is due to deviations of individual genotypic values at a site from the additive effects of site and genotype. In a practical sense GxE means that the relative performance of genotypes does not remain constant under all test conditions (Bridgewater and Stonecypher, 1978). These interactions can be due to actual changes in rank of the genotypes, differential changes in performance between genotypes in different environments but with no changes in rank or because of variability of the genetic component of variance at each site. It is important to differentiate between these causes of GxE as this will influence the subsequent decisions and strategy to be followed in dealing with the interactions (Barnes et al., 1984). Often researchers report the presence of GxE but the detection of a statistical difference is not in itself important, rather some measure of the loss of gain should be employed (Matheson and Raymond, 1986).

2.1.5 Heterogeneity of variance may contribute by increasing the estimates of GxE variance and should be identified and quantified (Lefkovitch, 1990), (Cooper and DeLacy, 1994). Estimates of GxE interaction variance is biased upward by heterogeneity of variance and correcting for this provides unbiased genetic correlations (Dickerson, 1962), (Eisen and Saxton, 1983).

2.1.6 The remaining interaction variance, once the effect of heterogeneity of variance has been removed, is due to a lack of correlation of genotypic performance among environments (Eisen and Saxton, 1983). This interaction variance is particularly important when this leads to re-ranking of genotypes (Cooper and DeLacy, 1994). It is the response which leads to re-ranking which impedes response to selection because it leads to a change in composition of the selected genotypes and thus will reduce overall genetic gain (Barnes et al., 1984), (Eisemann et al., 1990). It is important to make this distinction between these 2 sources of interaction and a number of statistical techniques have been utilized for this.

2.1.7 The ideal approach is to characterize test environments and identify main environmental factors that can be used to interpret the GxE (Skroppa, 1984). Work with *Pinus sylvestris* and *P.*

contorta in Sweden has suggested that clones or full-sib families ought to be used, depending on the environmental causes of the interaction (Gullberg, 1984). In some cases certain soil or other parameters have been identified which may then be utilized to deploy specific genotypes (Ronnberg-Wastljung and Gullberg, 1994). Often, the causes of interaction are not simply related to a single variable but rather to an index of several climatic or other factors (Alia et al., 1997), or to site quality (Hodge and White, 1992). Often large breeding zones are defined, and within these the GxE can be minimized. Work with Douglas Fir in Oregon, found little practical GxE within the large breeding zones set for the latter species (Johnson, 1997).

2.1.8 On the other hand, a study in Victoria with *Pinus radiata* suggested that often the apparent advantage of regional breeding calculations can be overestimated because the effect of variation between sites with a defined region is not considered (Pederick, 1990). In fact, the more common approach in breeding is to ignore or cope with the GxE by selecting stable, all-round good performers. Often these interactions are difficult to explain or define even when clear changes in rank between sites do occur (Raymond et al., 1997). In the latter study, with *Eucalyptus regnans* provenances in South Eastern Australia, one option considered was to select those provenances that perform reasonably well across all sites. Other studies with *Pinus taeda* (Li and McKeand, 1989), *Pinus tecunumanii* (Dvorak and Ross, 1994) and *P. radiata* (Johnson, 1992) suggest that the interaction is often due to only a few unstable, interactive families. In these cases the approach adopted is to ignore these unstable families and select only broadly adapted families that perform well on all sites. In a study in Queensland with *Pinus caribaea*, most of the GxE could be attributed to only one site and again in this case the approach adopted was to breed genotypes for the entire region rather than separate the area into sub-regions (Woolaston et al., 1991). In the *P. radiata* study alluded to above (Johnson, 1992), did suggest that potential loss in genetic gain was likely to be considerable when considering within-family selection. Indeed, GxE amongst clones has been demonstrated to be considerable in a number of studies (Bentzer et al., 1988), (Nielsen and Rouland, 1996), and in one study it was concluded that the GxE was increasing with age (Karlsson and Hogberg, 1998).

2.1.9 A further consideration is the effect of management induced changes on genotypes. Jahromi et al. (1976) found that different families of slash pine (*Pinus elliottii*) reacted differently under contrasting P incorporation and they concluded that selections should be conducted under nutrient regimes typical of the environment in which they will be deployed. Similar GxE was detected amongst *P. caribaea* families when the site was Cu deficient (Simpson et al., 1996). On the other hand no interaction was found amongst *P. taeda* families when contrasting fertilized and unfertilized conditions (Matziris and Zobel, 1976). Indeed, more recent studies GxE studies with *P. taeda* (McKeand et al., 1997) suggest that although there is no important rank change there

still is GxE. In this case the better families perform better on higher quality sites. They, and others (Duzan and Williams, 1988), thus suggest that the better families should be deployed on the better sites. This illustrates that understanding GxE for a particular species can have important management implications in other ways than alluded to above.

2.1.10 The GxE effects are real but to what extent are they useful? Can we utilize these to better improve the breeding and deployment of genotypes? For genotypes to be matched to sites, those sites must be well defined and repeatable (Matheson and Cotterill, 1990). This requires that we exactly define the important environmental factors. In most cases these are likely to be complex and may vary not only with environment, but also time, age and exact genotype. Some studies on slash pine suggest that the GxE decreases with age (Dieters et al., 1995). One solution is to adapt the breeding strategy so that the GxE can be utilized, without actually defining the environmental factors which cause this (Barnes, 1995). The latter author advocates a multiple population breeding strategy where the breeding population can be divided into sub-populations. These diversified populations would produce trees with different gene complexes in different environments and in this way exploit GxE. On the other hand, Hodge, (1996) suggests that some marginal gains are possible with regionalisation and that this depends on the extent of GxE.

2.2 Techniques for evaluating the Genotype x Environment interaction

2.2.1 Introduction

2.2.1.1 The basic requirements which are key to any study of GxE are replicated experiments, with numerous genetic entries and repeated in as many environments as possible (Shelbourne, 1972). In addition to the above requirement, any GxE study will need appropriate analysis of the data to determine the contributing environments and genotypes and thorough interpretation so that they may be of practical use in breeding strategy (Barnes et al., 1984). In this section many of the common statistical methods that have been utilized previously are identified and briefly evaluated. The intention is not to provide in depth details of each technique but rather to consider each in the light of the data available and assess which ones may be appropriate for this study.

2.2.1.2 To obtain a better understanding of the nature and amount of GxE a thorough statistical analysis should be undertaken. This may include both univariate and multivariate methods, some of which are identified and discussed below. A number of excellent reviews of many of these statistical methods, with reference to agricultural crops, have been done (Freeman, 1973), (Hill, 1975), (Westcott, 1986) and (Crossa, 1990). In addition, the subject has been extensively

covered in a number of recent books (Kang, 1990), (Gauch, 1992) and (Kang and Gauch, 1996). The following discussion will focus on some of the techniques which have been utilized successfully in tree breeding in an attempt to assess which methods may be of practical use in this study.

2.2.2 Ranking entry means and phenotypic correlations

2.2.2.1 Any study of GxE should begin with a thorough examination of data using simple comparative methods, including the use of some form of graphical representation to search for anomalies and likely contributors to any interaction (Barnes et al., 1984). A preliminary look at the entry means in each environment will reveal whether there are any rank changes or indeed differences in the relative performance of entries under different environments. Both of these may result in GxE (Falkenhagen, 1985; Matheson and Cotterill, 1990). On the other hand these differences in performance may simply be due to experimental error (Shelbourne, 1972).

2.2.2.2 Calculations of simple correlation coefficients between means in pairs of environments can be utilized as part of any preliminary study. The technique will provide a matrix of r-values that may give some indication of which environments differ from each other (Shelbourne, 1972). This technique has been utilized in a number of GxE studies.

2.2.3 Analysis of Variance

2.2.3.1 An analysis of variance (ANOVA) is usually the first, and most widely used, step in any statistical analysis of GxE data (Skroppa, 1984). An ANOVA allows the partitioning of total phenotypic variation into components due to genotype, environment, GxE interaction and error. The relative sizes of these variance components can then be used to quantify the magnitude of the GxE (Cooper and DeLacy, 1994). An interaction component proportionately 50% or more of the genetic component of variance, has been proposed as a point where loss of gain through selection could be compromised by the interaction (Shelbourne, 1972).

2.2.3.2 The environmental effects can be treated as fixed or random. If the environmental effects have been selected to represent particular 'known' variables then these can be regarded as fixed. However, in many cases environmental variation is unknown or unpredictable, and in this case the environment should be considered as random (Matheson and Raymond, 1986). These assumptions will impact on the expectation of mean squares in the analysis of variance.

2.2.3.3 A modified ANOVA has also been utilized where each environment and genotype in turn is omitted to determine the individual contributors to the GxE (Wricke, 1962), (Morgenstein and Teich, 1969) and the consistency of genotypes over all environments (Plaisted, 1960).

2.2.3.4 A significant interaction term in a multiple site experiment, using an ANOVA, does not in itself imply any practical significance (Matheson and Raymond, 1986). These interactions may be statistically significant but require further analysis to allow for better interpretation. An ANOVA can be regarded as a basis for further examination of the data (Shelbourne, 1972).

2.2.4 Regression analysis

2.2.4.1 In this technique the genotypic means at each site are regressed against the mean values of an environmental effect at each site (Matheson and Raymond, 1986). The technique was developed in an experiment with 277 barley varieties in South Australia (Finlay and Wilkinson, 1963), although it had also been used earlier (Yates and Cochran, 1938). For each barley variety, a linear regression of its yield in a given environment on the mean yield of all varieties in that environment was calculated. This allowed each genotype to be classified into one of four groups; high yielding, stable genotypes (high genotypic means with regression coefficients $b_1 < 1$); high yielding, unstable genotypes (high genotypic means with $b_1 > 1$); low yielding, stable genotypes (low genotypic means with $b_1 < 1$) and low yielding, unstable genotypes (low genotypic means with $b_1 > 1$). This technique is valuable for determining a genotype's stability over environments (Barnes et al., 1984).

2.2.4.2 This technique does have some limitations and has been criticized on statistical grounds. If an environmental index, representing an estimate of the true environmental effect is used, it can be subject to error (Freeman and Perkins, 1971) which can cause bias in estimating the regression coefficients (Hardwick and Wood, 1972). In addition, the same genotypes are used in the index that then are to be regressed on (Freeman, 1973). This latter objection has been alleviated by omitting the regressed genotypes or using other genotypes but in fact the practical significance of such modifications seems small (Snoad and Arthur, 1976). Finally, significance testing depends upon several assumptions which are not always met (Freeman, 1973). It is important to be aware of the conditional nature of statistical inferences, such as the fact that marginal means, both environmental and genotypic, should be regarded as fixed (Hill, 1975).

2.2.4.3 Despite all the above constraints, the joint regression analysis is probably the most frequently used method for evaluating GxE (Becker and Leon, 1988) and remains valuable for determining genotypic behavior over environments. In a comparison with several other methods,

it gave similar results and in addition it proved advantageous because it allowed for the prediction of performance in an untested environment (Barnes et al., 1984). It may also be utilized to regress genotypes onto any other physically measurable feature of the environment (Gibson, 1982), (Matheson and Raymond, 1984). Indeed it has been widely used in forestry experiments (Morgenstein and Teich, 1969), (Rehfeldt, 1979), (Gullberg and Vegerfors, 1987), (St.Clair and Kleinschmidt, 1986), (Bentzer et al., 1988), (Li and McKeand, 1989), (Woolaston et al., 1991), (Dvorak and Ross, 1994), (Alia et al., 1997), (Raymond et al., 1997).

2.2.5 Stability Analysis

2.2.5.1 Other techniques were developed to attempt to assign stability measures to genotypes. Initially these were developed using a modified ANOVA by omitting genotypes to determine the individual contributors to the GxE variance (Wricke, 1962). The latter author proposed the concept 'ecovalence'. Another approach looked at the consistency of genotypes over all environments (Plaisted, 1960). Further work along similar lines led to the assigning of a 'stability variance' which is calculated by partitioning the GxE into t components, one corresponding to each genotype. The sum of within and between environmental variance for each genotype would then define the 'stability variance' so that when this latter parameter is equal to the within environmental variance the genotype can be classed as stable (Shukla, 1972).

2.2.5.2 Several other techniques attempted to assign stability measures using a further development of the regression analysis (Eberhart and Russel, 1966), (Tai, 1971). They supplemented the regression coefficient with a second stability parameter using the mean square deviations from the regression line for each individual genetic entry. In another approach the regression coefficient and the deviation from the regression were also combined into a single stability measure (Hansen, 1970).

2.2.5.3 Several forestry studies have used variations of these stability analysis methods (St.Clair and Kleinschmidt, 1986), (Lima, 1987), (Nielson and Rouland, 1996). However, none of these techniques appear to offer any real advantages to the use of the joint regression analysis and in comparative studies the conclusions reached are similar (Barnes et al., 1984), (Matheson and Raymond, 1986).

2.2.6 Genetic correlations

2.2.6.1 Genetic correlations among traits indicate the degree to which one trait will change as a result of a change in another trait (Zobel and Talbert, 1984). Genetic correlations have generally

been estimated when both traits have been measured on the same individuals and these are termed Type A genetic correlations. Where 2 traits are measured on different individuals within genetic groups, for example a genetic correlation between trees of the same family grown in different environments, the correlation can be designated a Type B genetic correlation (Burdon, 1977). The concept has been developed and discussed extensively in the literature (Falconer, 1961), (Dickerson, 1962), (Yamada, 1962), (Eisen and Saxton, 1983), (Burdon, 1991), (Lu et al., 2001).

2.2.6.2 This concept was first suggested in work on mice raised in different environments where it was suggested that the performance within a single genetic group in separate environments could be regarded as 2 distinct traits (Falconer, 1961). It was later shown that these Type B genetic correlations could be derived both from conventional analysis of variance (Dickerson, 1962) and from using the latter, plus separate analysis of variance within each environment (Yamada, 1962). Essentially, this work showed that

$$rg_{xy} = \text{Cov } g_{xy} / (\sigma g_x \cdot \sigma g_y)$$

$$rg_{xy} = \text{Cov } (g_x g_y) / (\sigma g_x \cdot \sigma g_y)$$

where $\text{Cov } (g_x g_y)$ = covariance for groups between the trait as it is expressed in environments x and y respectively.

$\sigma^2 g_x$ and $\sigma^2 g_y$ are variances between groups at environments x and y respectively.

Relating the above to a conventional ANOVA if $\sigma^2 g_x = \sigma^2 g_y$ then

$rg_{xy} = \sigma^2 g / (\sigma^2 g + \sigma^2 g_e)$ where $\text{Cov } g_{xy} = \text{Cov } A_{xy}$ which = $\sigma^2 A = \sigma^2 g$ (Dickerson, 1962), (Burdon, 1977), (Yamada, 1962).

These concepts were used in a forestry context and it was suggested that the main attention, when considering GxE, should be given to the role of environments rather than genotypes (Burdon, 1977). It was suggested that in fact that the Type B genetic correlations could be a useful tool in quantifying the role of environments in generating interactions.

2.2.6.3 It has been correctly pointed out that the Type B genetic correlations estimated by using these methods could be biased or inaccurate when working with missing or very unbalanced data (Burdon, 1991). The use of multivariate methods to estimate the Type B genetic correlations can alleviate this to some extent, although the use of the so called Yamada II formula (see above) gave reasonable estimates provided the data was not too unbalanced (Lu et al., 2001). Multivariate methods can estimate genetic variances and covariances using the restricted maximum likelihood (REML) approach with an iterative procedure. Despite the above comments, genetic correlations have been widely used in forestry experiments (Burdon, 1977), (St.Clair and Kleinschmidt, 1986), (Bentzer et al., 1988), (Johnson and Burdon, 1990), (Carson, 1991),

(Woolaston et al., 1991), (Hodge and White, 1992), (Adams et al., 1994), (Dieters et al., 1995), (Hodge et al., 1995), (Beaulieu et al., 1996), (Dieters et al., 1996), (Haapenen, 1996), (Nielson and Roulund, 1996), (Johnson, 1997), (Hansen and Roulund, 1997), (Pswarayi et al., 1997), (Wu et al., 1997), (Hodge and Dvorak, 1999).

2.2.7 Multivariate methods

2.2.7.1 In addition to the univariate techniques described above, a number of multivariate methods have been utilized in GxE studies. These include principle component and principle coordinate analysis (Freeman and Dowker, 1973), (Garcia de Leon, 1982), (Campbell, 1986), (Gauch, 1988), (Li et al., 1997) and the Additive Main Effect and Multiplicative Model – AMMI (Gauch, 1988), (Cornelius, 1993), (Crossa et al., 1991), (Falkenhagen, 1996). The latter model is widely used in agriculture but only to a very limited extent in forestry. Indeed, it has been asserted that within forestry the AMMI has not brought any new insight over the traditional univariate methods mentioned above (Falkenhagen, 1996). This may, in part, be due to the fact that these techniques require many sites, and too often these have not been available in forestry experiments.

2.3 The utilization of GxE for maximum genetic gain

2.3.1 Dealing with GxE requires 5 distinct steps (Bridgewater and Stonecypher, 1978). These can be listed as follows:-

1. recognize its presence,
2. identify interacting environments,
3. identify interacting genotypes,
4. group the genetic entries and environments to partition GxE,
5. determine its potential impact.

It is the final two steps which are often the most difficult to achieve and thus often neglected and it is particularly this final step that is considered here. In addition to determining the impact of GxE, this section considers the other potential benefits of understanding the GxE for the species under study.

2.3.2 Perhaps most importantly it is necessary to compare the gains under different scenarios once an understanding of GxE has been gained (Shelbourne, 1972). This apparently simple task is made extremely complex because interactions have generally been found to be unrepeatable or, at the very least, poorly defined (Matheson and Cotterill, 1990), (Carson, 1991), (Johnson, 1997). However, there have been situations, particularly amongst provenance tests, where

causal environmental variables have been identified (Wright, 1973), (Gullberg, 1984), (Ronnberg-Wastljung and Gullberg, 1994) and (Alia et al., 1997). Under this scenario several methods have been suggested to compare gains with and without regionalisation (Burdon, 1977), (Matheson and Raymond, 1986), (Carson, 1991) and (Hodge, 1996).

2.3.3 Gain in one environment, by selecting in another environment can be calculated by utilizing the formula for correlated response to selection (Falconer, 1961). The use of the Type B genetic correlations for the above calculations was suggested and it was then a relatively simple matter to determine the efficiency of selecting in different environments relative to selecting over all environments or variations on these scenarios (Burdon, 1977). The latter author used Type B genetic correlations and standard formulae (Falconer, 1961) to present matrices of expected gain using actual figures from 3 sites. The results gave a range of gains per unit intensity of selection from 4.88 through to 1.31%. The former selected for planting on the same site and the latter selected at another site for planting on that site.

2.3.4 Another later proposal suggested that the actual loss of potential genetic gain was an appropriate indicator of the practical importance of GxE (Matheson and Raymond, 1984), (Lindgren, 1984). Genetic gain predicted assuming the interaction component of variance is present is divided by the genetic gain assuming no interaction. This ratio is then subtracted from the highest figure (= 1) and expressed as a percentage. This was termed the 'C' criterion by the former authors.

2.3.5 Predicted gains from selection were also calculated for various regionalisation options in New Zealand (Carson, 1991) using selection indices (Hazel, 1943), (Burdon, 1979). In each case, gains were calculated for breeding values on all sites and then restricting information from particular sites in order to determine the predicted gain to be calculated for that site without using information from that site. In this way comparisons using various gain option scenarios could be calculated. The study concluded that the small additional gains did not warrant regionalised breeding populations, especially as the gain calculated for some sites, represented by just one test, were not realisable. This latter observation was not taken into account in the relatively large gains suggested by (Burdon, 1977). Even within region the correlations between genotypic performance will never be one, thereby further decreasing gain.

2.3.6 The loss of potential genetic gain as a measure was also utilized using GxE estimates from Type B genetic correlations in *P. tecunumanii* (Hodge, 1996). In this approach separate breeding values for each region were predicted and compared to a combined breeding value under three GxE scenarios – high, moderate and low levels of GxE. The author then went to

compare the differences in genetic gain using a simple comparison of two equal regions, with the same selection intensity. Gains were always higher under a regionalisation scenario and varied between 0.2 – 3.5 %. The gains varied depending on the number of tests that were planted and the level of GxE that was predictable.

2.3.7 All of the above discussion assumes that a GxE quantified is predictable. In most situations this has not been the case and under these conditions breeders have opted for a single breeding population and selection for stability. However, another option suggested has been to utilize GxE empirically without actually attempting to define what it is in the environment that causes it (Barnes, 1995). In this approach, a multiple population strategy is advocated where broad indications of GxE is utilized to develop and build up populations matched to environments. The different sub-populations are utilized to create populations with different gene complexes that are adapted to different environments. In this way GxE can be exploited without actually defining its source.

2.4 An introduction to *Pinus patula*

2.4.1 *Pinus patula* originates in the mountainous regions of eastern and southern Mexico (Figure 2.1). It has a north to south distribution of approximately 900km occurring in the Sierra Madre Oriental and Sierra Madre del Sur between 24°N and 16°N (Dvorak, 1997). Its distribution is restricted and disjunct, occurring in temperate, humid regions within this defined area (Poynton, 1979).

2.4.2 The species falls within the section Serotinae, subsection Oocarpae (Price et al., 1998), although revisions to this have been made often in the last few years (Perry, 1991; Farjon and Styles, 1997). The latest studies have suggested that the pine species most closely related to *P. patula* are *P. greggii*, *P. pringlei*, *P. jaliscana*, *P. herrerae* and *P. teocote* [Dvorak, 1999 #155]. *P. patula* is composed of two varieties, namely: *Pinus patula* Schiede ex Schlecht. & Cham. var. *patula* and *Pinus patula* Schiede ex Schlecht. & Cham. var. *longipedunculata* Loock ex Martínez [Dvorak, 2000 #534]. *P. patula* var. *patula* grows in a relatively narrow band on the eastern escarpment of the Sierra Madre Oriental, from the state of Tamaulipas in the north, at 24°N latitude, to northeastern Oaxaca, at 17°N latitude (Perry, 1991). It includes all the provenances from Conrado Castillo in the north, to Santa Maria Papalo in the south. *P. patula* var. *longipedunculata* occurs sympatrically with the former variety in northeastern Oaxaca and has been identified as far south as 16°N in Sierra Madre del Sur of southwestern Oaxaca [Dvorak, 2000 #534]. This variety includes the provenances of Ixtlán in the northeast and El Tlacuache to the southwest. It is important to bear in mind the existence and differences of these two varieties

in any discussion of genotype x environment interaction (GxE), as material from both taxa are considered in this study. The two varieties can be distinguished geographically, morphologically and genetically [Dvorak, 1999 #155]. However, unless otherwise stated, the two varieties will simply be referred to as *P. patula* in the discussions that follow.

2.4.3 In the Sierra Madre Oriental, *P. patula* tends to be found on the moister, eastern slopes (Wormald, 1975). The altitude varies from around 1500 to just under 3000m (Table 1). The species can often grow in pure dense stands, although it can be associated with other species such as *Pinus greggii* and *P. teocote* as well as several other hardwoods (Barrett, 1972).

2.4.4 The habitat and ecology of the species has been thoroughly covered in two publications (Vela, 1980)[Dvorak, 2000 #534]. The summary presented below draws heavily from these latter two publications and covers only as much detail as is seen as pertinent to the objectives of this study. The species occupy sites that can best be described as moist/temperate to sub-humid/temperate montane habitats.

2.4.5 The annual precipitation as represented by the CAMCORE provenance collections vary from 1000mm to 2500mm (Table 2.5.1). The major portion of this tends to fall mainly in summer (May to October in the northern hemisphere). The winters are generally characterized by a distinct dry season. However, even during this dry season most sites receive some moisture in the form of clouds and fog. In fact, the distribution of the species in essence mirrors the presence of the cloud belt. Above about 3000m the humidity drops and other conifers and broadleaf species replace *P. patula*, whereas below this belt at around 1500m, temperatures increase, fog and rain fall off and other pines such as *P. greggii* and *P. teocote* can outcompete it.

2.4.6 Mean annual temperature range for the species varies from 10 – 18°C with temperatures in winter dropping to well below zero on many sites. The number of frost days varies from 5 to 101, with a trend towards warmer, more moderate temperatures on those sites present in the southern state of Oaxaca, particularly in those provenances occurring in the mountains of the Sierra Madre del Sur.

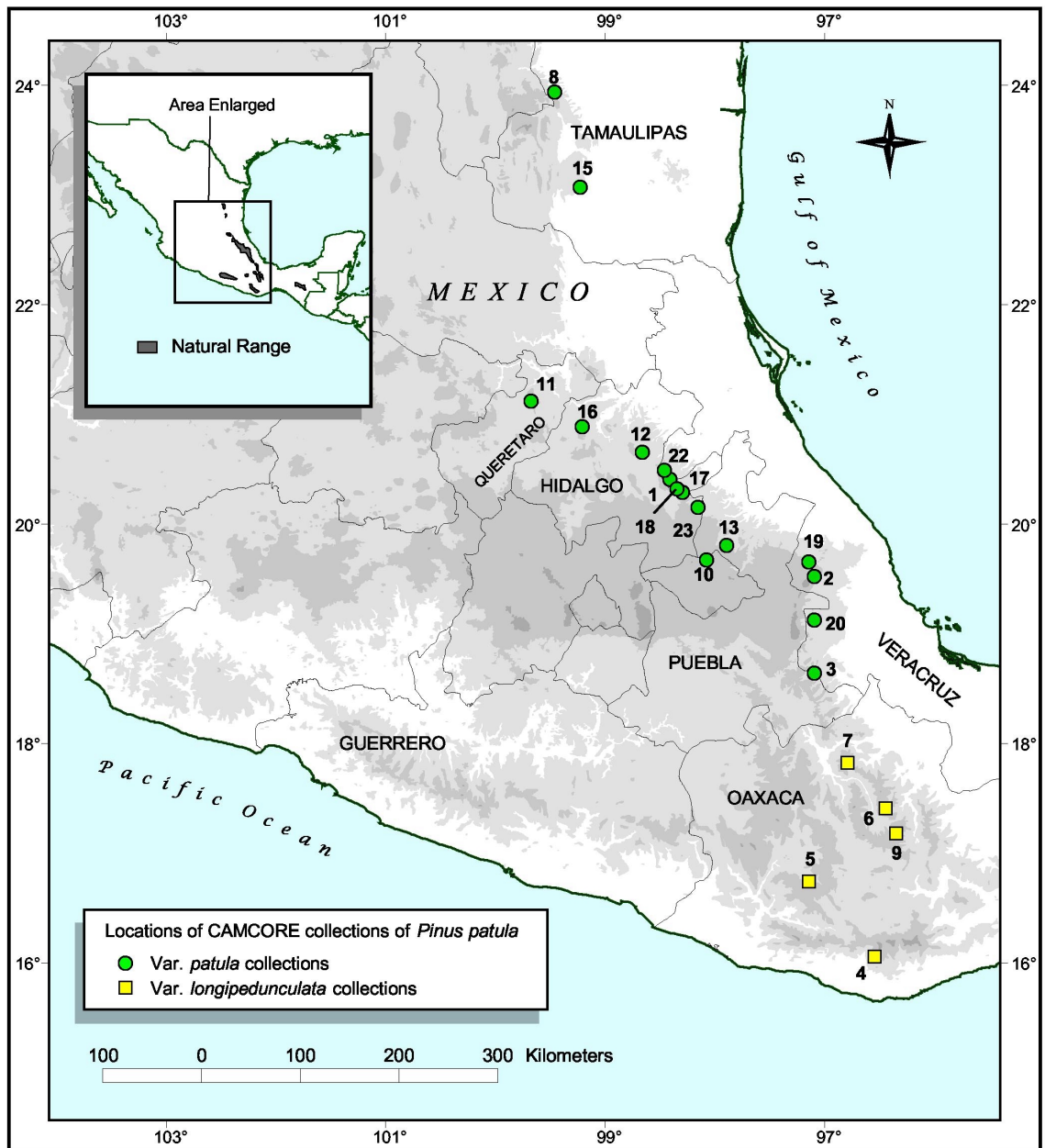


Figure 2.5.1: Distribution of *P. patula* in Mexico and location of CAMCORE collection sites in the region

2.4.7 *P. patula* tends to grow on deep, well-drained soils. The soils, in a study of 14 soil profiles in areas where *P. patula* was growing, varied from 60cm to between 1 and 2m in depth and in pH between 4.8 and 6.4 in the A horizon (Vela, 1980). The species is generally found on Alfisols but sometimes also occurs on more degraded and shallow Ultisols and Inceptisols [Dvorak, 2000 #534]. Generally, even within the cloud belt region, as soils become shallower, *P. patula* gives way to *P. teocote* or oak species.

2.4.8 Fires play an important role in the ecology of the species. *P. patula* is an aggressive pioneer species which can rapidly colonize gaps created by amongst other agents, fires [Dvorak, 2000 #534]. The species is able to exploit these gaps and form dense pine thickets with a very high stocking. This prevents other undergrowth from becoming established and creates a humid environment within the stand, thus minimizing the risk of fires. As the stand gets older some mortality occurs which creates gaps for the intrusion of other hardwoods and undergrowth. Furthermore, older trees have thicker bark, which enables them to survive low intensity fires to some degree.

2.4.9 The species has been established in pilot plantings in over 20 countries in the tropics and subtropics since the late 1900's (Wormald, 1975). Approximately 1.0 million hectares of plantation have been established worldwide (Birks and Barnes, 1991). Commercial plantings are present in both Latin America and Africa. Africa alone has over 0.5 million hectares (Borota, 1991), with the majority of the plantations found in southern and eastern Africa. South Africa has around 376 000ha of *P. patula* plantations which equates to fully 47% of all softwoods planted and just under 25% of the total area established to commercial forestry in the country (Department of Water Affairs and Forestry, 1998). It is possibly, after *Pinus radiata*, the most widely tried species in the tropics and subtropics [Dvorak, 2000 #534].

2.4.10 In South Africa, *Pinus patula* is the most widely distributed softwood planted operationally in the summer rainfall regions (Department of Water Affairs and Forestry, 1998). Viable commercial plantations of the species exist in the region from the Hogsback, in the Eastern Cape province, at a latitude 30°35'S to the Soutpansberg mountains of the Northern Province at 22°58'S (Bester, 2000). Within this latitudinal range, *P. patula* plantations are generally restricted to the moister, eastern areas associated with an escarpment that runs roughly north/south through the region. These forests have largely replaced low growing, seasonally dormant, grassland (Versveld et al., 1994), and occupy areas where rainfall is generally around 700mm or more per year. The wood of *P. patula* is utilized both for sawn lumber (Wright, 1994), as well as for pulpwood. It is extensively utilized as a raw product for mechanical pulping (Wright and Sluis-Cremer, 1992) and in the manufacture of Kraft pulp (Morris et al., 1997).

2.4.11 The exact origin of the first early importations of *P. patula* seed from Mexico into South Africa, between 1909 and 1931 are uncertain. Most of the original seed imported came from only three small commercial collections amounting to only around 15kg (Wormald, 1975). This is postulated to have come from the areas in the central range of the species distribution in Mexico, possibly Hidalgo and northern Oaxaca (Burgers, 1975), (Olesen, 1972). In 1969, seed collected from superior individuals in the Mexican States of Puebla, Hidalgo and Oaxaca were imported into South Africa (Darrow and Coetzee, 1983), and at the same time the Zimbabwe Forestry Commission received eight provenances from Mexico (Barnes and Mullin, 1984). These were planted in a series of progeny/provenance trials in South Africa and Zimbabwe respectively. Some seed from further provenance collections made by the FAO in the early 1980's were also planted out in South Africa (F.A.O., 1982).

2.4.12 During the mid1980's the Central America and Mexico Coniferous Resources Cooperative (CAMCORE), based at North Carolina State University, Raleigh, USA, made systematic range-wide seed collections within Mexico (Donahue, 1989). These collections, plus an additional provenance collection in 1995 (CAMCORE, 1995), sampled populations throughout the known geographic range of the species. This material has been established in a comprehensive set of trials, covering range of sites in Southern Africa, Colombia and Brazil.

2.4.13 Despite all these additional introductions, most of the current deployment and breeding populations originated from the seed initially imported between 1910 and 1913 and there was thus some concern that the genetic base of the landrace of the species in South Africa was too narrow. An isozyme study comparing a selected South African population with a population selected from the natural range of the species in Mexico, suggested that the genetic variation was similar between the two populations (Butterfield, 1990).

2.4.14 Genetic improvement with *P. patula* in the region was initiated, both in Zimbabwe (Mullin, 1990) and South Africa (Poynton, 1979), in the late 1950's. *P. patula* breeding initially involved the selection of plus trees within the unimproved plantations and the grafting of these trees into Clonal Seed Orchards. These trees were then progeny tested and, on the basis of these results, the orchards were rogued (Mullin, 1990). These initial studies have been used to assess the genetic parameters for this species in Southern Africa and are generally consistent with the findings emanating from the CAMCORE provenance/progeny tests (Dvorak, 1997).

2.4.15 Individual tree heritability estimates increase from around 0.11 at three years to around 0.2 at eight years (Barnes et al., 1992), (Barnes et al., 1992), (Nyoka et al., 1994), (Dvorak, 1997). Age-age genetic correlations were found to be very high for growth traits between three,

five and eight years. In a study in Zimbabwe, using controlled cross experiments Barnes, (1992) found strong juvenile-mature correlations. The genetic correlations between height and basal area in the second and eighth years were very high (between 0.6 and 1). The genetic correlations for volume growth at age five with that of age eight was found to be 0.87 in the CAMCORE trials (CAMCORE, 1997), 0.94 and even as high as 1.0 in Zimbabwe (Barnes et al., 1992), (Nyoka et al., 1994).

2.4.16 Numerous reports of an interaction for growth traits between *P. patula* genotypes and different environments have been reported and these are discussed in more detail further on in this chapter.

2.5 Site, silviculture and growth of *P. patula*

2.5.1 Introduction

2.5.1.1 The capacity of a tree species to establish and grow successfully is influenced by a complex range of many fluctuating and interacting factors, which include both internal (physiological) and external (environmental) variables. All of these together determine forest productivity (Pritchett and Fisher, 1987). Many of the environmental factors can be measured to a greater or lesser extent and a better understanding of how these influence tree growth on a species level should provide some guidance on those that may be important on a within-species level. A discussion around those variables that have been shown to be of importance with *P. patula* in the sub-region follows.

2.5.1.2 Environmental variables can broadly be divided into biotic and physical (abiotic) components (Remezov and Pogrebnyak, 1969). The biotic factors include genetic differences, intraspecific competition (as influenced by stand density), interspecific competition (which in forestry terms when considering a crop can be referred to as weed competition), pests and diseases. Many of the biotic factors can be impacted by management and thus form an important facet of silvicultural research. Genetic differences are considered as a given and are the central focus of this study, and as such are not considered further here.

2.5.2 Stand density

2.5.2.1 Intraspecific competition has a major influence on tree growth. Trees in closed stands compete with each other above ground for light and growing space, and below ground for moisture, nutrients and oxygen.

2.5.2.2 The volume per hectare is much greater when there are more trees per unit area, before the crowns close. This situation is reversed when considering the volume on a per tree basis (Oliver and Larson, 1990). The radial growth of trees is strongly impacted by spacing, whereas height growth is generally regarded as relatively insensitive to spacing (Lanner, 1985). A brief summary of the situation with *P. patula* is given below.

2.5.2.3 The mean height of trees is relatively unaffected by planting density (von Gadow and Bredankamp, 1992), (Morris, 1995), (Morris, 1995). However, some studies have reported that stand density has a curvilinear relationship with height (von Laar, 1978), (Morris, 1996), and one study concluded that mean height increases with decreasing stocking and that this effect becomes more apparent with increasing site quality (von Gadow, 1983).

2.5.2.4 The diameter growth of trees is strongly affected by density. Mean diameter per tree decreased with increasing planting density but stand basal area per hectare increased (von Gadow, 1983). However, if one examines the diameter distribution, although the mean tree diameter decreases this does not seem to affect the trees with very large diameter. Thus, the larger, dominant trees seem to be relatively unaffected by the increased stocking. This phenomenon has been reported for *P. patula*, both in Southern Africa (Morris, 1995) and Colombia (Osorio and Uribe, 1994).

2.5.2.5 In all spacing studies, mortality is impacted by the level of stocking. Mortality is curvilinearly related to stand density and the higher the stocking, the earlier the advent of density dependent mortality (von Laar, 1978). At densities of between 1300 to 1600 stems per hectare, which is the density commonly utilized for pulpwood crops in Southern Africa, mortality generally commenced between the ages of 8 to 15 years of age (Morris, 1995). Interestingly, significant amounts of mortality at these latter stockings have been reported to be associated with periods of drought (Morris, 1995) and were also impacted by silvicultural treatments such as fertilization or site preparation (Morris, 1996). Normally, a high site index is associated with a low potential to carry great numbers of live trees. This reported relationship does not always hold with *P. patula*, in that some sites supporting good height growth were also associated with a high capacity to carry many live trees (von Gadow, 1983).

2.5.2.6 In many plant species grown at high densities, including coniferous trees, a relationship between volume or biomass and mortality exists known as the $-2/3$ power law (Hutchings, 1983). This is the so called "self-thinning rule" which suggests that for any given mean diameter, in even aged stands, there is a limit to the number of live trees per hectare which may coexist. In *P.*

patula, studies of a range of spacing studies have suggested that the slope of the self-thinning line may differ for different sites (von Gadow, 1986).

2.5.2.7 Volume is a function of height and diameter. Due to the relative insensitivity of height to differences in stand density, volume behaves in a similar fashion to diameter growth. Mean tree volume decreases with increased stocking, whereas volume per unit area increases (von Laar, 1978). Thus stands planted at relatively high densities have been suggested for pulpwood crops grown for 16 years without thinning. A stocking of 2430 stems per hectare for maximum volume production has been suggested (Bredankamp, 1980). This is supported by (Morris, 1996) who reported volume increases when planting densities were increased from 820 to 1770 trees/ha.

2.5.2.8 Stand density also significantly influenced the stem form and branching of *P. patula*. For a given dbh and height, stem form improved with increasing stand density (von Laar, 1978). Moreover, in the same study, branch volume per tree and the mean diameter of the 10 percent thickest branches were significantly related to stand density.

2.5.3 Interspecific competition

2.5.3.1 Interspecific competition involves adverse interference among plants of different species. These plants would thus be in competition with the tree crop, and can be regarded as weeds. The impact of weed competition on the growth and survival of pines has been clearly demonstrated such as in *P. radiata* (Richardson, 1993) and (Sands and Nambiar, 1984), *P. taeda* (Miller et al., 1991), and *P. elliotii* (Shiver et al., 1994). In a managed plantation environment, competition with weeds is most acute before canopy closure, although woody species may interact with trees throughout stand growth (Minogue et al., 1991). Little work has been done with *P. patula* in this field and what has been done is briefly summarized below.

2.5.3.2 Studies on the impact of weeds on survival of *P. patula* have been contradictory. In some situations, survival was improved by weed control (Ramsden, 1992), (Christie, 1994) and indeed in one study, the species was found to be more sensitive to weed competition than *P. elliotii* (Schumann, 1992). However, several other studies have not shown any impact on survival with increased weed competition (Morris, 1994), (Morris, 1994), (Rolando and Little, 2000).

2.5.3.3 Several studies have indicated that the early growth of *P. patula* is significantly reduced by weed competition (Morris, 1994), (Morris, 1994), (Christie, 1994), (Rolando and Little, 2000). However, none of the studies have yet demonstrated that these growth differences are

maintained through to rotation age. *P. patula* has been reported to be relatively more sensitive to weed competition than other species (Little, 1998). In the latter study the species recorded the greatest loss of diameter growth, when compared to *P. taeda* and *P. elliotii*, despite having lower percentage weed cover. This effect is, however, not universally apparent. In a separate species x silviculture trial on a weedy, low elevation site, the response to weed control was of the same proportion for all seven species under test (Morris, 1994).

2.5.4 Pest and diseases

2.5.4.1 A number of pests and diseases have been reported in *P. patula* plantations throughout the regions where it is planted. The intention here is not too extensively review this topic but rather to look briefly at some of the important pests and diseases which affect the species and highlight how certain environmental conditions often play an important role in influencing the severity of the infestation.

2.5.4.2 The two most serious diseases in Southern Africa are *Sphaeropsis sapinea* and *Rhizinia undulata* (Wingfield and Swart, 1994). The former species also seriously infects *P. patula* in Southern Brazil [Dvorak, 2000 #534]. *P. patula* is also known to be susceptible to *Fusarium circinatum* f. sp. pini (Pitch Canker) in the nursery, although as yet no mature trees have shown symptoms of the disease (Viljoen et al., 1994). In addition, damage is also caused by a range of insect pests. The most important of these are *Hylastes angustatus* (Atkinson and Govender, 1997), *Glena* spp. [Dvorak, 2000 #534], and a number of aphids (Madoffe and Austara, 1990).

2.5.4.3 In South Africa *S. sapinea* often enters trees after some other external damage, most commonly hail, has wounded the host tissue (Wingfield and Roux, 2000). Indeed, this disease has limited the area currently planted to *P. patula* to the cooler, higher lying areas in Southern Africa. The reason given is that at lower elevations the risk of experiencing warm, humid conditions favorable for the disease increases. In Brazil, on the other hand, no wounding seems necessary, yet higher at elevations in that country damage caused by the disease is also reduced [Dvorak, 2000 #534].

2.5.4.4 *R. undulata* is stimulated by heat, and moist, warm weather provides ideal conditions for the fruiting structures (Wingfield and Roux, 2000). The pathogen causes wide scale mortality in both seedlings and older trees after fires. Obvious management strategies to prevent infection include the discontinuation of burning after clearfelling and the delay of replanting for several months if fires have occurred. The former strategy has however resulted in the build up of root

feeding insects such as *H. angustatus* in the slash. These pests have been implicated as a cause of severe mortality in seedlings of *P. patula* (Atkinson and Govender, 1997).

2.5.5 Site Requirements for *P. patula*

2.5.5.1 The physical (abiotic) components affecting tree growth can be grouped into climatic, physiographic and edaphic (Pritchett and Fisher, 1987). These factors can often be measured with a reasonable degree of accuracy and are often related to site quality and hence tree growth. All of the above three components can be split into a large number of variables that will not be considered individually here. Rather, only those variables which have been shown to be important in influencing tree growth will be discussed, particularly in the context of the studies involving *P. patula*.

2.5.5.2 The process of defining what is suitable for the growth of trees can be looked at within a hierarchy, representing a series of levels. Perhaps the first level could be attempting to define the requirements for the growth of forests in general. This assumes considerable importance in Southern Africa where large areas are too dry to support trees (Versveld et al., 1994). In addition, the nature of the mountainous terrain results in rapid changes in climate with distance (Jackson, 1974). Many studies have looked at the factors important for the establishment of a commercial tree crop in the sub-region and all agree that aerial climate, and rainfall in particular, are important factors (King, 1951), (Poynton, 1971), (Schonau and Schulze, 1984). More recently several authors have also emphasized the importance of a range of soil properties as determinants of tree growth (Schonau and Fitzpatrick, 1981), (Grey et al., 1987). Underlying both climate and soil factors is the soil moisture availability. In Southern African forest sites water availability is often limited, while evaporative demand is high (Roberts, 1994). Furthermore, many of the forest soils of the region are inherently low in fertility since they occur on ancient weathering surfaces in high rainfall areas (Olbrich et al., 1997).

2.5.5.3 The choice of species is one of the most important decisions influencing the success of a forest crop (Zobel and Talbert, 1984). This can be regarded as the next level in the hierarchy referred to above, and in effect this represents the first stage in any GxE study. The GxE, referred to here can be regarded as macro-interactions where the differences between genotypes and between environments are very large (Matheson and Cotterill, 1990). It has been suggested in general terms that soil moisture availability and temperature are the factors with which species most commonly interact (Barnes et al., 1984).

2.5.5.4 In Mexico, the distribution of *P. patula* mirrors the occurrence of the fog and cloud belt, and within this, the distribution is defined by soil depth. The soils on which the species occurs tend to be deep and well drained (Vela, 1980). On an international, broad scale, the site requirements for *P. patula* have been described as deep, well drained soils, with an annual rainfall greater than 850mm, latitudes between 18° to 30°, and within that latitudinal band, at altitudes above 1000m, increasing to above 2200m if growing the species nearer the equator [Dvorak, 2000 #534].

2.5.5.5 In the Southern African region, more specifically, numerous authors have defined and refined the species niche (Kotze, 1926), (Poynton, 1957), (Poynton, 1966), (Barrett and Mullin, 1968), (Esterhuysen, 1985), (Schonau and Grey, 1987), (Schutz, 1994). The species requirements emphasized by many of the authors include a reference to rainfall or moisture availability, altitude, adaptation to frost and snow, a moderate drought tolerance, the presence of mist, a preference for moderate to deep, well drained soils and a wide tolerance to exposure. All the studies have emphasized that the species should only be planted in the summer rainfall areas and that it does not tolerate wet soils. One author even suggests that some 'very high' rainfall sites may be 'too wet' for the species (Schutz, 1994).

2.5.5.6 Most recently, the species niche for *P. patula*, in the sub-region, has been broadly defined as requiring mean annual temperatures less than 18°C and an annual rainfall requirement of 700mm at high altitudes and 950mm elsewhere (Morris and Pallett, 2000). In addition, the latter authors have again emphasized the relative tolerance to frost and snow and cautioned against the planting of the species at lower elevations due to the risk of hail induced damage from the fungal pathogen *Sphaeropsis sapinea* and in areas with poorly drained soils.

2.5.6 Factors impacting on the yield of *P. patula*

2.5.6.1 Site factor studies seek to predict the yield for a species on a specific site. The main approach is to determine quantitative relationships between measured environmental variables and tree growth. These site factor studies have two key objectives (Louw, 1999); The prediction of potential tree growth in unplanted areas or where information on alternative species is required, and to attempt to identify those factors within the environment which relate to tree growth. The site factor studies carried out on *P. patula* are reviewed in an attempt to highlight or identify those factors that are related to or determine the growth of the species. It is not considered unreasonable to utilize these factors as a starting point when searching for those environmental variables which may be important in determining GxE amongst genotypes within the species.

2.5.6.2 Clearly, the site factors assessed rarely measure the primary influences on tree growth adequately. Factors such as light intensity and duration, temperature, water availability and CO₂ concentration for example are likely to be of prime importance but are not easily measured. In the field it is usually necessary to resort to secondary factors of a site, which can be assessed, such as elevation, aspect, and soil moisture content, to name but three. It is then assumed that these are correlated with the former, primary factors.

2.5.6.3 Only one site factor study has been carried out within indigenous stands of the species in Mexico (Castanos, 1962). The study was focused on the stands of *P. patula* in Northern Oaxaca and examined site index in relation to twenty-two site factors. The equation derived, which explained almost 53 percent of the observed variation, contained three factors, total soil depth, aspect, and elevation.

2.5.6.4 In southern Africa, a number of such site factor studies have been carried out on the species within plantations (Evans, 1974), (Grey, 1979), (Schonau and Wilhelmij, 1981), (Schutz, 1990), (Louw, 1995) and (Zwolinski et al., 1998). Each of these studies was done within a limited area with relatively homogenous or recurring patterns of site factors. With increasingly larger geographical areas, there is likely to be a decrease in correspondence between Site Index and site factors (Louw, 1999). This should be borne in mind when considering a GxE study over a region wide area. The underlying physiological mechanisms that influence how the trees interact with the environment need to be carefully considered.

2.5.6.5 Two circumstances present in plantations, as opposed to natural forests, such as the study carried out in Mexico and alluded to above, are likely to contribute to a greater degree of precision in attempting to determine differences due to site. Firstly, the silviculture and management of stands tend to be relatively uniform within a given area, and secondly, sampling can be restricted to stands within a narrow age range. Thus any growth differences can be more precisely attributed to site rather than crop treatment or age of the trees (Evans, 1974).

2.5.6.6 A study in the Usutu forests of Swaziland used top height as the dependent variable and site factors as the independent variables (Evans, 1974). A large range of site variables was measured which included topographic, edaphic and climatic factors. The results showed that the growth of *P. patula* was strongly influenced by topography and soil, and three factors in particular were important: elevation above sea level, distance from ridge and soil set. In terms of elevation, a pronounced curvilinear relationship was shown and the author suggested that this probably

reflected the influence of climate, in particular the interrelationship between temperature and amount of P in the subsoil and the exchangeable K in the topsoil.

2.5.6.7 Other site factor studies carried out in other regions within Southern Africa have found similar results with various variables identified which serve as surrogate indicators of important variables influencing the growth of the species. In another study carried out in the Umzimkulu District of the KwaZulu-Natal Province of South Africa (Grey, 1979), similar variables such as altitude and percentage distance from ridge crest were found to be important. The latter author also showed that slope percentage, slope shape, aspect and land surface could be related to tree growth and suggested that these factors all influenced the water regime and soil processes present on the sites and in this way influenced tree growth (Carmean, 1975). The study indicated that soil factors were consistently less satisfactory indicators for growth prediction than topographic variates but some general trends were noted. Namely, A-horizon factors were better predictors than those in the B-horizon and factors assessed in the C-horizon were poorest. In addition, soil depth factors were less useful indicators than chemical factors associated with the A-horizon.

2.5.6.8 Other site factor studies in South Africa have identified a number of other site variables as influencing tree growth in the species. Mean annual precipitation and the South African classification of soil form showed a weak relationship in a study within the KwaZulu-Natal midlands of South Africa (Schonau and Wilhelmij, 1981). Two further comprehensive studies in the Mpumalanga province of South Africa identified geology, terrain position, effective rooting depth, exchangeable Ca and fine sand in the top soil, stone content in the subsoil and driest quarter precipitation as significantly related to tree growth (Schutz, 1990), (Louw, 1995). These two Mpumalanga studies were able to predict between 74 and 84 percent of the variation using the latter site variables as well as those referred to in the earlier studies. Most recently, in the Eastern Cape Province, in what represents the most southern site factor study with *P. patula*, in addition to mean annual precipitation and effective rooting depth, soil water holding capacity was identified as an additional site variable (Zwolinski et al., 1998).

2.5.6.9 Several other more recent studies have tested a large range of variables to try to explain the growth of *Pinus patula* using inventory data. The use of many of these variables has become easier through the advent of more powerful computers and effective software packages utilizing a GIS (Geographic Information System) platform. Examples of some of these variables include mean slope, mean aspect, weighted mean effective soil depth, maximum temperature of the hottest month and driest quarter precipitation. The variation explained with the use of subsets of these variables never amounted to more than 70 per cent (Strydom, 2000), (Pallett, 2001).

2.5.7 Growth characteristics of *Pinus patula*

2.5.7.1 A brief description of the growth habits of *P. patula* in South Africa is given. A thorough knowledge of these characteristics may aid in gaining a better understanding of how the species interacts with the environment and whether some particular growth traits are associated with greater adaptability.

2.5.7.2 The species grows to between 20 and 30m in height, occasionally reaching 40m. It generally has a straight bole and may retain apical dominance up to an age of around 30 years, although trees with a higher branch angle tend to lose apical dominance and become round headed (Wormald, 1975). The lateral branches are whorled with pendulous secondary branches.

2.5.7.3 A study in the Mpumalanga province of South Africa showed *P. patula* to be multinodal with up to 3 internodes on the same shoot showing simultaneous growth (Norskov-Lauritsen, 1963). Node formation occurred in two phases, a late season phase (March to May) with new shoot initials formed prior to winter and a mid-season phase (December to February), where new shoot initials are formed after extension of the late season initials (Olbrich, 1993). Growth ceased or slowed down for two months between June and August, with absolute dormancy being often less than one month in duration (Norskov-Lauritsen, 1963). Moreover, shoot elongation occurred in two phases, a short fast phase from August to October, and a longer, slower phase of growth between November to April or even May (Olbrich, 1993).

2.5.7.4 The duration of the latter elongation phase varied and was dependent on tree age, with older trees having shorter internode lengths and producing fewer internodes per season (Norskov-Lauritsen, 1963). In another study in the Usutu Forest of Swaziland, current annual height increment was related to the growth habits of the species (Evans, 1978). Current annual height increment increased rapidly to a maximum in about the 4th year of growth. This was paralleled by the number of internodes produced annually, and rather more erratically by internode length. The number of internodes produced reached a maximum in year 4 at around five internodes and decreased progressively to around four at age 7 years, three at age 12 and dropping to only one internode per year at 20 years of age (Evans, 1978). The average internode length also increased from 1 to 5 years, at which time the average length was around 0.44 meters.

2.5.7.5 The initiation of the growth flush after winter was recorded as starting simultaneously at two locations, 45km apart, and at markedly differing altitudes of 950m and 1520m (Payn et al.,

1989). It was suggested that temperature or day length influenced the first growth flush after winter.

2.5.7.6 Needle extension occurred mainly during the mid to late season of growth, from December to May, after the phase of rapid shoot extension was over (Olbrich, 1993). Leaf senescence occurs when the oldest needles start to yellow in mid to late season (January to April) with needle fall occurring over a long period throughout the late season into the early season of the following year (Olbrich, 1993). Needles may persist for 17 months right up to 4 years and occur in fascicles of 3 or 4 with individual needle lengths ranging between 15 and 30cm. Stomata are present on all surfaces of the leaf (Wormald, 1975).

2.5.7.7 Many of the growth models alluded to earlier incorporate rainfall as important determinants of the growth of *P. patula*. A study using detailed stem analysis data over a number of years (Evans, 1978) showed that low rainfall over two consecutive years had a dramatic effect on the growth of a range of stands of varying ages. Moreover, it has been asserted that the distribution of rainfall and the length of the dry season may also be important parameters influencing growth (Poynton, 1979). These effects are paralleled by observations in a detailed study within a fertilizer trial in the Mpumalanga province of South Africa, where trees from fertilized and unfertilized plots were assessed regularly over a two-year period (Olbrich, 1993). The author suggested that tree growth in response to rainfall could be best interpreted by contrasting branch length increment of the trees assessed.

2.6 Genotype x environment interactions with *P. patula*

2.6.1 Numerous reports of a genotype x environment interaction within the species have been reported, both within Southern Africa (Denison, 1973), (Falkenhagen, 1979), (Barnes et al., 1992), (Snedden and Verry, 1999) and in Colombia (Ladrach and Lambeth, 1991). The studies referred to within the sub-region have all been either from Zimbabwe or from the Mpumalanga province in the northeastern part of South Africa. In reality *P. patula* is now planted over a far greater range, both in Swaziland, to the south east and into the provinces of Kwa-Zulu Natal and the Eastern Cape, to the south. In this review, each of the reports is described and the relative GxE reported below.

2.6.2 The earliest reported study of two sites in the Mpumalanga province reported significant family x locality interaction for a number of traits including growth, branching and cone production (Denison, 1973). In these trials, families originating from both Zimbabwe and South Africa were tested on two sites in Mpumalanga. Generally, the local South African material was performing

better on both sites, suggesting that the material selected locally was 'better adapted' to the local environment. Both sites were situated only 16km apart and differed mainly in elevation, the distribution of rainfall, and soils. The assessments were carried out at 3 years and indicated a Type B genetic correlation of 0.58.

2.6.3 In 1969 seed from 13 pine species were collected from Mexico, and the individual progenies kept separate. Twenty-eight families of *P. patula* were collected from 4 locations, namely from the states of Oaxaca, Puebla and two locations in Hidalgo. The seedlings were planted on 5 sites in the Mpumalanga province of South Africa and the results of assessments on 4 of the trials, carried out at 6 years were reported (Falkenhagen, 1979). On two of the sites a 6x7 rectangular lattice design was used and a highly significant trial by progeny interaction was found with the rankings of families changing significantly between trials. Climate apparently had a strong influence on the ranking of the seedlots (Darrow and Coetzee, 1983). Generally, the families from Hidalgo tended to perform better on the cooler, more temperate, high elevation site whereas those from Oaxaca on the lower elevation, warmer site. Based on growth characteristics alone, no families were selected from the southern Oaxacan sources at the high elevation site whereas almost half the selections came from this source at the warmer site.

2.6.4 In contrast to the above, another study of 42 OP families across 2 sites suggested that the genotypes performed in a relatively stable manner (Van Wyk and Falkenhagen, 1984). In this case the assessments were made around 5 years of age and the two sites were located in two distinct zones and differed in elevation, mean annual rainfall and soils. Nevertheless, the authors did point out that the magnitude of the GxE component of variance was at least as large as the family component and suggested that stratification and the development of regional breeding populations was necessary in South Africa..

2.6.5 A study in Columbia on two sites also reported significant GxE (Ladrach and Lambeth, 1991). The study included OP selections from their own plantations in Colombia as well as seed from plus trees selected in South Africa. The two sites varied in altitude (2500 and 3050m), rainfall (3050 and 1200mm) and latitude (2° 30' and 5°10'N). The lower site was selected as a 'typical' site for growing the species where growth was expected to be good, whereas the second site was described as being at high elevation near the 'tree line' and at the maximum limit for reforestation. The rank correlation between sites for seventh year volume was very low ($r=0.18$) and not significant. They concluded that GxE was important and would need to be considered, but pointed out that the good performance of the South African selections in Colombia suggested that material selected in one region could be of importance when planted elsewhere.

2.6.6 A further comprehensive study in Zimbabwe using polycross, factorial and diallel mating designs on 4 sites also reported GxE for volume traits but none for wood density (Barnes et al., 1992; Barnes et al., 1992). The GxE interaction variance was reported to be of practical significance and was, on average, between a third and a half of that contributed by GCA (Barnes et al., 1992). A repeatability of performance of genotype over environment was calculated as an intra-class correlation ($R_e = \text{variance of effect} / \text{variance of effect plus variance of the interaction of the effect with environment}$) (Barnes and Schweppenhauser, 1979). Over two or more localities equates to a Type B genetic correlation. The Type B correlations for volume at 8 years at the two main sites, was calculated as 0.93 for the polycross and 0.53 for the factorial tests. Some of the tests were also repeated over consecutive years and no genotype-year interaction was detected. This latter finding has important implications because it suggests that, unlike agricultural crops, the year by year environmental variations may not be as important for this species and indeed for trees in general.

2.6.7 A later study, again in the Mpumalanga province of South Africa, looked at the GxE across 5 sites using open-pollinated and polymix families (Snedden and Verry, 1999). Growth, as well as stem and crown form was considered. The material available in one trial set allowed comparison between two sites, Jessievale, a 'typical' highveld or high elevation site, and Tweefontein, regarded as a 'typical' middleveld or medium elevation site. In a separate trial series, the middleveld site at Tweefontein and three other sites at similar or lower elevation, were compared. A significant site, family, and family by site interaction was reported for all trials in all traits with the significance of the interaction for volume highest between the high and middleveld sites. Genetic correlations were calculated for all pairs of sites and the relationship between the high and middleveld sites suggested a moderate correlation with evidence of some rank changes. A regression of family means between the latter two sites gave a highly significant fit ($p=0.0001$) but nevertheless a relatively low R^2 (0.25). A comparison between the other 4 sites situated at lower elevation suggested that the GxE was less and could be attributed more to a 'fanning' response, or a scale effect, rather than any rank changes. Genetic correlations between pairs of sites here were found to be moderate to good (0.56 - 0.72). The authors concluded that the breeding population be established on two sites on the middle and lowveld and that a low selection intensity be used on this breeding population when making selections for the highveld (Snedden and Verry, 1999).

2.6.8 An overall analysis of the CAMCORE *P. patula* progeny/provenance trials, performed across 3 countries and incorporating data from 64 tests aged between 3 and 8 years has revealed an unusual pattern (Hodge, 2000). The average within-country Type B genetic correlations, and Type B provenance correlations are fairly typical for forest trees ($r_{Bg} = 0.68$ & r_{Bp}

= 0.58 respectively). However, when comparing across countries, provenances performed very differently ($r_{BP} = 0.23$), with these differences being related to latitude, elevation and precipitation. Overall, in Colombia the provenances from the southern state of Oaxaca performed best, whereas in South Africa the best provenances were from the northern part of the range in Veracruz, Hidalgo and Tamaulipas. The Type B provenance correlation between South Africa and Columbia was 0 whereas that between Brazil and South Africa was 0.40. However, within provenance, the Type B genetic correlations between countries was much higher, and suggested that families within a provenance were relatively more stable ($r_{Bg} = 0.66$ & 0.55 between South Africa / Brazil and South Africa / Columbia respectively).

2.6.9 The relative instability of performance of some of the different *P. patula* provenances in southern Africa has been reported on a number of occasions (Falkenhagen, 1979; Darrow and Coetzee, 1983; Kanzler, 1994). On the whole in South Africa, sources from the central to northern part of the range of *P. patula* have been reported to perform best (Dvorak et al., 1995; Hodge, 2000). In contrast, on some sites, sources from the southern, Oaxaca areas of Mexico have been reported to perform better, relative to the northern sources. These sites have been at Usutu, Swaziland (Kanzler, 1994) and at Tweefontein, Mpumalanga (Falkenhagen, 1979; Darrow and Coetzee, 1983). Both of these sites are at relatively lower elevation or are associated with a warmer, milder climate than the more 'typical' sites where *P. patula* is grown in South Africa. A series of provenance trials on six sites were also established in Zimbabwe in 1971 (Barnes and Mullin, 1984). Zimbabwe is situated further to the north and these sites are likely to represent a more tropical environment than those in South Africa. The results of these trials showed that none of the imported material was performing as well as the improved seed orchard sources from Zimbabwe, but nevertheless it was suggested that sources from the more southern provenances be sampled and could be of considerable potential in that country. The southern Oaxacan sources have also been reported to grow better in Colombia than other sources [Dvorak, 2000 #534] (Hodge, 2000), and this has also been attributed to the generally more tropical nature of the climate there when compared with South Africa in general.

**CHAPTER 3 – GENOTYPE X ENVIRONMENT INTERACTION IN A SERIES OF
PROVENANCE / PROGENY TRIALS OF *PINUS PATULA* IN SOUTH AFRICA**

(Published as Genotype x environment interaction in a series of provenance / progeny trials of *Pinus patula* in South Africa in Proceedings of IUFRO Conference 'Forest Genetics for the next Millennium', Durban, South Africa, Institute for Commercial Forestry Research. 2000)

Chapter Summary

Introduction

Materials and Methods

Results and Discussion

Literature Cited

Genotype X Environment Interaction in a Series of Provenance/Progeny trials of *Pinus patula* in South Africa

Abstract

The type and magnitude of genotype x environment interactions in *Pinus patula* in Southern Africa is examined. *P. patula* is by far the most important softwood species grown in the region and is being deployed operationally almost entirely using improved, orchard grade seed. Breeding with this species has been ongoing for over 40 years and is moving into the 3rd cycle of selection. Several studies within the sub-region have indicated that genotype x environment interaction is present amongst families, and provenances. Furthermore, the species is grown on a wide range of site types and recently some companies have started to deploy vegetatively propagated families operationally. The emphasis on this latter aspect is likely to increase and could ultimately result in the deployment of clonal material. All of the above suggests that genotype x environment interaction is likely to become increasingly important in the future. CAMCORE, based at NC State, North Carolina, USA, has been distributing seed to four member companies within the sub-region since the late 1980's and those members have planted a series of structured tests which presented an opportunity to study this question in greater detail. This paper quantifies the extent of genotype x environment interactions present, and attempts to identify causal environmental factors, within the sub-region, as represented by a range of CAMCORE trials.

Keywords: *Pinus patula*, genotype x environment interaction, South Africa

Arnulf Kanzler¹ & Gary R. Hodge² 29 October, 1999

¹ Sappi Forest Research, Shaw Research Centre, P. O. Box 473, Howick, 3290, South Africa.

Tel: +27 333 302455 Fax: +27 333 304938 Email: arnulfk@za.sappi.com

² CAMCORE, North Carolina State University, Box 7626, NC 27695, Raleigh, North Carolina, USA.

Tel: +1 919 5156424 Fax: +1 919 5156430 Email: grh@unity.ncsu.edu

INTRODUCTION

In South Africa, commercial plantation forestry is practiced on around 1.5 million hectares and supplies a market which produces both pulp and paper, as well as a large sawtimber industry (Dept. of Water Affairs and Forestry, 1998). The opportunity for expansion of this forest base is, however, severely limited and probably, realistically represents only a few hundred thousand more hectares (Versfeld et al., 1994). This situation places increasing demands on foresters to examine ways of improving the productivity of the existing forest landbase. Site-specific silviculture and in particular more efficient genotype x site matching represents an opportunity to achieve these objectives. The plantation area in the country is divided roughly equally between hardwoods and softwoods and *Pinus patula* represents around half of all softwoods planted in region. The species is utilized, for both sawlog and pulpwood purposes and due to favorable wood properties for those markets, in addition to good growth, is planted widely in the sub-region. It is commercially restricted to the summer rainfall region and the total area planted equates to around 375 000ha. *P. patula* was introduced into the region in the early part of this century (Burgers, 1975) and active breeding within the species began in the 1950's (Wormald, 1975). It's range extends in latitude from 18°40S in Zimbabwe to 31°00S in the Eastern Cape Province of South Africa, in elevation between 1000 and 2000m and in rainfall from 750 to more than 1800mm of rainfall per year.

The genetic improvement within *P. patula* has been successful with significant improvement in both stem form and growth being achieved. Realized gains in volume have been assessed in genetic gain trials and equal between 10 and 18% for seed orchard mixes and up to 40% for the best families (Stanger, 1998). In addition, good progress has been made in site-species matching and several studies have successfully defined and later refined the niche over which *P. patula* should be planted (Evans, 1974, Schutz, 1990 and Pallett, 2000). However, despite several studies reporting the presence of GxE, little progress has been made at better evaluating the impact and significance within the defined species niche. In an earlier study across two sites (Denison, 1973), indicated the presence of a significant family by location interaction, for volume growth at three years, and suggested that locally bred South African seed sources were better adapted to the growing conditions of the test locations than material imported from Zimbabwe. Other later studies, (Falkenhagen, 1979 and Barnes, et. al., 1992) also demonstrated the presence of a significant GxE interaction. None of these studies, however, attempted to quantify this GxE, nor investigate its causes or implications. Finally, a more recent study, established over 5 sites in the Mpumalanga province of South Africa (Snedden & Verryn, 1999), showed that moderate levels of GxE were present. They demonstrated genetic correlations between sites of 0.51 to 0.73 and recommended that a single breeding population be established on two sites and the selection intensity be low enough to allow selections for specific regions after testing in those regions. They related the GxE to altitude and defined the regions as low, middle and highveld. They suggested that the GxE was partially a function of the different responses of the trees at different altitudes, with those at lower altitudes having heavier branching and poorer stem form.

Genotype x environment interaction results when the relative performance of genotypes differs when grown in different environments (Zobel and Talbert, 1984). This can be expressed symbolically in the following simple model:

$$P = G + E + GE$$
 (where P = phenotypic value, G = the genetic effect, E = an environmental effect, and GE = an effect due to GxE.)

Generally genetic and site effects are much stronger than the genetic-site interaction (Wright, 1973). Furthermore, it is difficult and expensive to manage and therefore it is not surprising that its potential to increase production has been ignored by many breeders (Barnes, 1984). The dilemma, is that on the one hand GxE tends to hamper progress in breeding by necessitating more replications in space and/or time, while on the other hand a strong interaction offers opportunity to increase gains by developing specific genotypes which will do well in specific environments (Squillace, 1969). Certainly the success in bridging the gap between demonstrating the presence of GxE in forest tree breeding, and utilizing this information for maximum benefit has rarely been achieved. Often the constraint has been identifying and quantifying the important environmental variables responsible for the GxE and at the same time demonstrating the repeatability of the responses. In this study the level of GxE is quantified and assessed and an attempt is made to link these interactions with selected environmental variables considered important for *Pinus patula*.

MATERIALS AND METHODS

Twenty-two provenances of *P. patula* were sampled in Mexico by the CAMCORE Cooperative between 1986 and 1991 (Dvorak and Donahue, 1992). The collection sites range in latitude from 16°06' N to 23°56' N, in elevation from 1500m to 2915m and in mean annual precipitation between 1000mm and 2000mm (Table 1). In each provenance, seeds were collected from approximately 10 – 30 mother trees that were selected for good volume growth and stem straightness. This seed was kept separate by mother tree and within the Southern African region these seed collections were distributed to three CAMCORE member companies (Safri – now Safcol, Mondi and Sappi). A total of 33 tests containing over 81000 trees were established (Table 2). The trial design was the same at all locations, a randomized complete block design, with provenances randomized in each replication, and families randomized within the provenance sub-plots. There were 9 replications and 6 trees per family planted in row-plots per replication giving a total of 54 plants per family per test. All trees were planted at an espacement of 3m x 3m in each test.

Test assessments were done at 3, 5, and 8 years of age and all trees were measured at each assessment. In this paper only growth measurements will be reported although several other traits such as stem straightness and stem form were also recorded. Growth traits measured included height in meters and diameter at breast height at a level of 1.3m (DBH) in centimeters. A volume index was calculated using height and DBH with the formula:-
Volume = 0.00003 (DBH² * height).

As a part of the data preparation, a plot of height x DBH was inspected visually. Trees which were outliers (i.e. those which had abnormal height-diameter ratios) were deleted from the data set. Thus, trees with heights severely affected by top breakage were not included in the volume calculations or analysis.

Single site analysis

For each test, single site analyses were conducted using the linear model as follows:

$$Y_{ijklm} = \mu_i + B_j + P_k + F(P)_{kl} + B^*F(P)_{jkl} + \epsilon_{ijklm}$$

Where, Y_{ijklm} phenotypic observation for the $ijklm^{\text{th}}$ tree,

μ_i = mean in the i^{th} test,

B_j = fixed effect of the j^{th} block,

P_k = random effect of the k^{th} provenance, $E[P_k] = 0$, $\text{Var}[P_k] = \sigma_p^2$,

$F(P)_{kl}$ = random effect of the l^{th} family in the k^{th} provenance, $E[F(P)_{kl}] = 0$, $\text{Var}[F(P)_{kl}] = \sigma_F^2$,

$B^*F(P)_{jkl}$ = random effect of the jkl^{th} row-plot, i.e. the interaction of the j^{th} block with the l^{th} family within the k^{th} provenance, $E[B^*F(P)_{jkl}] = 0$, $\text{Var}[B^*F(P)_{jkl}] = \sigma_{b^*f(p)}^2$,

ϵ_{ijklm} = random error term associated with the $ijklm^{\text{th}}$ tree, $E[\epsilon_{ijklm}] = 0$, $\text{Var}[\epsilon_{ijklm}] = \sigma_e^2$.

Table 1: Summary of the CAMCORE *Pinus patula* provenance collections included in these tests*

Provenance	Prov Code	State	Lat	Long	Alt. (m)	MAP (mm)	Test representation
Carrizal de Bravo	CDB	Guerrero	17°35'N	99°51'W	1980-2440	1209	20-10-07B1, 20-10-07B2
Cumbre Muridores	CM	Higdalgo	20°19'N	98°21'W	2380-2480	1860	20-10-08A, 20-10-08B, 20-07-09B, 20-18-09A
La Cruz	LC	Higdalgo	20°17'N	98°18'W	2300-2450	1869	20-10-08A, 20-10-08B, 20-07-09B, 20-18-09A
La Encarnación	LE	Higdalgo	20°45'N	99°13'W	2400-2650	1200	20-10-08A, 20-10-08B, 20-07-09B, 20-18-09A
Zacualtipán	ZA	Higdalgo	20°39'N	98°40'W	1980-2200	2047	20-07-05L, 20-10-05E1, 20-10-05E2, 20-10-05F, 20-18-05K, 20-07-06E, 20-10-06B1, 20-10-06B2, 20-18-06D, 20-07-07D, 20-10-07B1, 20-10-07B2, 20-18-07A
Cuajimoloyas	CU	Oaxaca	17°11'N	96°26'W	2450-2770	1135	20-07-07D, 20-10-07B1, 20-10-07B2, 20-18-07A
El Manzanal	EM	Oaxaca	16°06'N	96°33'W	2350-2660	1348	20-07-02D, 20-10-02A, 20-10-02B, 20-18-02E, 20-10-03A1, 20-10-03A2
El Tlacuache	ET	Oaxaca	16°44'N	97°09'W	2300-2620	2000	20-07-02D, 20-10-02A, 20-10-02B, 20-18-02E, 20-10-03A1, 20-10-03A2
Ixtlán	IX	Oaxaca	17°24'N	96°27'W	2600-2870	1750	20-07-02D, 20-10-02A, 20-10-02B, 20-18-02E, 20-10-03A1, 20-10-03A2
Santa Maria Papalo	SMP	Oaxaca	17°49'N	96°48'W	2270-2720	1100	20-07-02D, 20-10-02A, 20-10-02B, 20-18-02E, 20-10-03A1, 20-10-03A2
Pinal de Amoles	PA	Queretaro	21°07'N	99°41'W	2380-2550	1350	20-07-05L, 20-10-05E1, 20-10-05E2, 20-10-05F, 20-18-05K, 20-07-06E, 20-10-06B1, 20-10-06B2, 20-18-06D, 20-07-07D, 20-10-07B1, 20-10-07B2, 20-18-07A
Llano Las Carmonas	LLC	Puebla	19°48'N	97°54'W	2530-2880	1097	20-07-05L, 20-10-05E1, 20-10-05E2, 20-10-05F, 20-18-05K, 20-07-06E, 20-10-06B1, 20-10-06B2, 20-18-06D, 20-07-07D, 20-10-07B1, 20-10-07B2, 20-18-07A
Conrado Castillo	CC	Tamaulipas	23°56'N	99°28'W	1500-2060	1012	20-07-05L, 20-10-05E1, 20-10-05E2, 20-10-05F, 20-18-05K, 20-07-06E, 20-10-06B1, 20-10-06B2, 20-18-06D, 20-07-07D, 20-10-07B1, 20-10-07B2, 20-18-07A

El Cielo Tlacotala	EC TL	Tamaulipas Tlaxcala	23 ^o 04'N 19 ^o 40'N	99 ^o 14'W 98 ^o 05'W	1600-1730 2750-2915	1200 1097	20-10-08A, 20-10-08B, 20-07-09B, 20-18-09A 20-07-05L, 20-10-05E1, 20-10-05E2, 20-10-05F, 20-18-05K, 20-07-06E, 20-10-06B1, 20-10-06B2, 20-18-06D, 20-07-07D, 20-10-07B1, 20-10-07B2, 20-18-07A
Corralitla	CO	Veracruz	18 ^o 38'N	97 ^o 06'W	2000-2230	1500	20-07-01L, 20-10-01A, 20-10-01B, 20-18-01H, 20- 18-01J, 20-10-03A1, 20-10-03A2, 20-07-04C, 20- 10-04A1, 20-10-04A2
Cruz Blanca	CB	Veracruz	19 ^o 39'N	97 ^o 09'W	2500	1347	20-10-08A, 20-10-08B
Ingenio del Rosario	IR	Veracruz	19 ^o 31'N	97 ^o 06'W	2770-2870	1346	20-07-01L, 20-10-01A, 20-10-01B, 20-18-01H, 20- 18-01J, 20-07-04C, 20-10-04A1, 20-10-04A2
Potrero de Monroy	PM	Veracruz	20 ^o 24'N	98 ^o 25'W	2320-2480	1350	At least 2 families included in all tests except 20-10- 07B2 & 20-07-09B
Manzanares	MZ	Veracruz	19 ^o 39'N	97 ^o 08'W	2400-2450	1295	20-07-10B, 20-10-10C
Calchualco	CA	Veracruz	19 ^o 07'N	97 ^o 06'W	2350-2400	2020	20-07-10B, 20-10-10C
Magueyes	MA	Veracruz	18 ^o 53'N	97 ^o 16'W	2250-2350	1200	20-07-10B, 20-10-10C, 20-18-10E

*Details from Dvorak & Donahue, 1992

Variance components for all traits were estimated using the PROC MIXED procedure in SAS. The phenotypic variance within-provenance (σ^2_T) was estimated as follows:-

$$\sigma^2_T = \sigma^2_F + \sigma^2_{b \cdot f(p)} + \sigma^2_e$$

Single-site heritability estimates within provenance (h^2_b) were estimated for all growth traits assessed, and for all tests separately, using the formula:

$$h^2_b = \frac{3 \sigma^2_F}{\sigma^2_T}$$

A coefficient of 3 instead of 4 was multiplied by the family variance to give an estimate of the additive genetic variance. There are two reasons why this assumption was made. Firstly, there was some likelihood that some of the progeny emanating from the mother trees in natural stands were inbred due to the presence of neighboring, related trees in the stand, and secondly it is likely that some of the open-pollinated families were not truly half-sibs, but contained some full-sibs (Squillace, 1974). The "b (p)" subscript indicates that the family variance is estimated on a within provenance level and on a single-site basis and may be biased upward by the presence of family x environment interaction. The family variance component estimated using data from a single site includes both the family variance ($\sigma^2_{f(p)}$) and a variance due to the interaction of family and site ($\sigma^2_{f(p)e}$). If this was estimated using a multiple site model, i.e. $\sigma^2_{F(p)} = \sigma^2_{f(p)} + \sigma^2_{f(p)e}$ (Comstock and Moll, 1963 and Hodge and White, 1992), the component of variance due to the interaction of family with environment can be identified.

Paired site analysis

Paired site analyses were conducted for all possible pairs of tests. The only restrictions were that the tests should have at least 15 families in common, and that the single-site, within-provenance heritability (h^2_b), calculated according to the method outlined above, should be greater than 0.05 for both tests. These analyses were conducted in order to quantify the level of genotype x environment interaction (GEI) present both among families and provenances, and establish the existence of any relationships between this GEI and selected environmental variables present.

The analyses were conducted in two different ways. In the first method both the provenance and family effects were identified and kept separate, with the family effect being within provenance. The linear model used in this first analysis was as follows:

$$Y_{ijklm} = \mu + E_i + B(E)_{ij} + P_k + P^*E_{ik} + f(P)_{kl} + f(P)^*E_{ikl} + r_{ijkl} + \epsilon_{ijklm}$$

Where, Y_{ijklm} = phenotypic observation for the $ijklm^{th}$ tree,
 μ = overall grand mean

E_i = fixed effect of the i^{th} test,
 $B(E)_{ij}$ = fixed effect of the j^{th} block nested within the i^{th} test,
 P_k = random effect of the k^{th} provenance, $E[P_k] = 0$, $\text{Var}[P_k] = \sigma_p^2$,
 P^*E_{ik} = random interaction of the k^{th} provenance with the i^{th} test, $E(P^*E_{ik}) = 0$, $\text{Var}(P^*E_{ik}) = \sigma_{pe}^2$,
 $f(P)_{kl}$ = random effect of the l^{th} family in the k^{th} provenance, $E[f(P)_{kl}] = 0$, $\text{Var}[f(P)_{kl}] = \sigma_{f(p)}^2$,
 $f(P)^*E_{ikl}$ = random effect of the interaction of the l^{th} family within the k^{th} provenance across the i^{th} test, $E[f(P)^*E_{ikl}] = 0$, $\text{Var}[f(P)^*E_{ikl}] = \sigma_{f(p)e}^2$,
 r_{ijkl} = random effect of the $ijkl^{\text{th}}$ row-plot, i.e. the interaction of the j^{th} block within the i^{th} test with the l^{th} family within the k^{th} provenance, $E[r_{ijkl}] = 0$, $\text{Var}[r_{ijkl}] = \sigma_r^2$
 ϵ_{ijklm} = random error term associated with the $ijklm^{\text{th}}$ tree, $E[\epsilon_{ijklm}] = 0$, $\text{Var}[\epsilon_{ijklm}] = \sigma_e^2$.

In the second approach the provenance effect was ignored and thus all variation due to genetic effects at both provenance and family level was pooled. In this latter case the linear model was as follows:

$$Y_{ijkl} = \mu + E_i + B(E)_{ij} + f_k + f^*E_{ik} + f^*B(E)_{ijk} + \epsilon_{ijkl}$$

Where, Y_{ijkl} = phenotypic observation for the $ijkl^{\text{th}}$ tree,

μ = overall grand mean
 E_i = fixed effect the i^{th} test,
 $B(E)_{ij}$ = fixed effect of the j^{th} block nested within the i^{th} test,
 f_k = random effect of the k^{th} family, $E[f_k] = 0$, $\text{Var}[f_k] = \sigma_f^2$,
 f^*E_{ik} = random effect of the interaction of the k^{th} family within the i^{th} test, $E[f^*E_{ik}] = 0$, $\text{Var}[f^*E_{ik}] = \sigma_{fe}^2$,
 $f^*B(E)_{ijk}$ = random effect of the ijk^{th} row-plot, i.e. the interaction of the j^{th} block within the i^{th} test with the l^{th} family, $E[f^*B(E)_{ijk}] = 0$, $\text{Var}[f^*B(E)_{ijk}] = \sigma_r^2$
 ϵ_{ijkl} = random error term associated with the $ijkl^{\text{th}}$ tree, $E[\epsilon_{ijkl}] = 0$, $\text{Var}[\epsilon_{ijkl}] = \sigma_e^2$.

For each pair of tests, and for each method, estimates of type B genetic correlations were calculated. In the first method estimates at the family and provenance levels ($r_{Bg(p)}$ and r_{Bp} respectively) were calculated as follows:-

$$r_{Bg(p)} = \frac{\sigma_{f(p)}^2}{\sigma_{f(p)}^2 + \sigma_{pe}^2}$$

$$r_{Bp} = \frac{\sigma_p^2}{\sigma_p^2 + \sigma_{pe}^2}$$

Table 2: Summary information for CAMCORE *P. patula* tests in South Africa, included in Analysis

Obs	Test code	Region	Location	Lat.	Long.	Alt.	MAP	MAT	Age	Nr. Family(prov)
						(m)	(mm)	(°C)	(yrs)	Representation**
1	20-18-01J	N.E.Cape	Commonage	31°02'S	28°19'E	1480	757	14.7	8	PM(16), IR(14), CO(16), CON(5)
2	20-18-02E		Commonage	31°02'S	28°19'E	1480	757	14.7	8	PM(3), EM(13), ET(11), IX(15), SMP(14), CON(5)
3	20-18-05K		Commonage	31°02'S	28°19'E	1480	757	14.7	8	PM(3), CC(16), TL(4), PA(15), ZA(9), LLC(8), CON(5)
4	20-18-06D		Commonage	31°02'S	28°19'E	1480	757	14.7	8	PM(3), CC(7), TL(2), PA(7), ZA(2), LLC(7), CON(5)
5	20-18-07A		Commonage	31°02'S	28°19'E	1480	757	14.7	8	PM(3), CC(5), TL(4), PA(6), ZA(2), LLC(8), CU((3), CON(5)
6	20-07-01L	Kwa-ZuluNtl	Maxwell	30°02'S	29°56'E	1350	817	16	8	PM(17), IR(14), CO(16), CON(5)
7	20-07-02D		Maxwell	30°02'S	29°56'E	1350	817	16	8	PM(3), EM(12), ET(11), IX(15), SMP(14), CON(5)

8	20-07-05L	Maxwell	30°02'S	29°56'E	1350	817	16	8	PM(3), CC(16), TL(5), PA(15), ZA(8), LLC(8), CON(5)	
9	20-07-06E	Maxwell	30°02'S	29°56'E	1350	817	16	8	PM(3), CC(8), TL(4), PA(7), ZA(1), LLC(8), CON(5)	
10	20-07-07D	Maxwell	30°02'S	29°56'E	1350	817	16	8	PM(3), CC(5), TL(4), PA(6), ZA(2), LLC(8), CU(3), CON(5)	
11	20-07-04C	Mpumalanga	Helvetia	25°32'S	30°22'E	1700	770	14.7	3	PM(15), IR(10), CO(10), CON(5)
12	20-07-09B		Helvetia	25°32'S	30°22'E	1700	770	14.7	3	EC(18), LE(5), LC(12), CM(16), CON(5)
13	20-07-10B	Helvetia	25°32'S	30°22'E	1700	770	14.7	3	PM(5), MZ(13), CA(13), MA(20), CON(5)	
14	20-10-01A	Tweefontein	25°03'S	30°46'E	1150	1274		8	PM(18), IR(16), CO(16), CON(5)	
15	20-10-02A	Tweefontein	25°03'S	30°46'E	1150	1274		8	PM(3), EM(12), ET(11), IX(16), SMP(15), CON(5)	
16	20-10-03A1	Tweefontein	25°03'S	30°46'E	1150	1274		8	PM(3), EM(11), ET(11), IX(10), SMP(13), CO(1), CON(5)	
17	20-10-04A1	Tweefontein	25°03'S	30°46'E	1150	1274		8	PM(13), IR(10), CO(9), CON(5)	
18	20-10-05E1	Tweefontein	25°03'S	30°46'E	1150	1274		8	PM(3), CC(17), TL(5), PA(15), ZA(9), LLC(10), CON(5)	
19	20-10-06B1	Tweefontein	25°03'S	30°46'E	1150	1274		8	PM(3), CC(9), TL(10), PA(7), ZA(2), LLC(12), CON(5)	
20	20-10-07B1	Tweefontein	25°03'S	30°46'E	1150	1274		8	PM(3), CC(5), TL(7), PA(7), ZA(3), LLC(9), CU(9), CDB(2), CON(5)	
21	20-10-08A	Tweefontein	25°03'S	30°46'E	1150	1274		5	PM(7), EC(10), LE(9), LC(10), CM(10), CB(8), CON(3)	
22	20-10-10C	Tweefontein	25°03'S	30°46'E	1150	1274		8	PM(5), MZ(10), CA(13), MA(19), CON(5)	
23	20-10-01B	Jessievale	26°14'S	30°31'E	1730	921	14	8	PM(16), IR(14), CO(16), CON(5)	
24	20-10-02B	Jessievale	26°14'S	30°31'E	1730	921	14	8	PM(3), EM(12), ET(11), IX(15), SMP(15), CON(5)	
25	20-10-03A2	Jessievale	26°14'S	30°31'E	1730	921	14	8	PM(3), EM(9), ET(10), IX(7), SMP(9), CO(1), CON(5)	
26	20-10-04A2	Jessievale	26°14'S	30°31'E	1730	921	14	8	PM(13), IR(8), CO(9), CON(5)	
27	20-10-05E2	Jessievale	26°14'S	30°31'E	1730	921	14	8	PM(2), CC(17), TL(4), PA(15), ZA(8), LLC(8), CON(5)	
28	20-10-06B2	Jessievale	26°14'S	30°31'E	1730	921	14	8	PM(2), CC(8), TL(3), PA(7), ZA(1), LLC(10), CON(5)	
29	20-10-07B2	Jessievale	26°14'S	30°31'E	1730	921	14	8	CC(4), TL(2), PA(6), ZA(2), LLC(6), CU(2), CDB(1), CON(5)	
30	20-10-05F	Mariti	24°55'S	30°57'E	980	1316		5	PM(5), CC(17), TL(6), PA(15), ZA(11), LLC(10), CON(3)	
31	20-18-01H	Jessievale	26°12'S	30°29'E	1691	931	14	5	PM(19), IR(17), CO(15), CON(5)	
32	20-18-08B	Jessievale	26°12'S	30°29'E	1691	931	14	5	PM(8), EC(10), LE(9), LC(10), CM(9), CB(8), CON(5)	
33	20-18-09A	Jessievale	26°12'S	30°29'E	1691	931	14	5	EC(17), LE(5), LC(12), CM(17), CON(5)	

**CON represents other controls.

For the second method, an aggregate family-provenance type B correlation (r_{Bg}) at the level, defined as the family in the model, was similarly calculated as follows:-

$$r_{Bg} = \frac{\sigma_f^2}{\sigma_f^2 + \sigma_{fe}^2}$$

These type B correlations, calculated in three ways above, measure the genetic, provenance or aggregate family-provenance correlation between the same trait expressed on two different sites (Burdon, 1977). Type B genetic correlations range between 0 and 1. An r_{Bg} of 1 would indicate a perfect correlation between the behavior of genotypes (or provenances) on both sites and suggest the complete absence of GxE. Parameter means and empirical standard errors were calculated using each pair of tests as an independent observation.

The type B genetic parameter estimates were then utilized to test the importance of selected environmental variables such as geographic regions, mean annual precipitation, mean

annual temperatures, site quality and a parameter defined as climate index. In each case the 'environment' defined, was grouped into three categories (Table 3), and each type B correlation parameter estimate, representing a measure of the 'similarity' or otherwise, between two sites, as measured by the behavior of similar genotypes on both sites was used as an individual observation. Each type B correlation estimate was thus grouped into sites defined as 'similar' and those defined as 'different'. The degree in which the correlations concurred with the artificially defined environmental parameter groupings was then assessed using an analysis of variance approach where the environmental categories were regarded as fixed effects in the model.

Table 3: 'Environmental parameters' utilized to test the similarity, or otherwise, between pairs of sites using the type B correlation parameter estimates calculated for all possible combinations. Each 'environmental parameter' was categorised into three classes as defined below.

Environmental parameter	Major categories	Possible combinations tested
Geographic Region (REG)	North-Eastern Cape Province (C) Kwazulu- Natal Province (N) Mpumalanga Province (M)	CC = both sites within the C CN = one site situated in N the other in C and similarly for CM, NN, NM & MM
Mean annual Precipitation (MAP)	High with a MAP > 1000mm (H) Medium with a MAP 850-1000mm (M) Low with a MAP < 850mm (L)	HH = both sites with rainfall > 1000mm HM = one site with high, the other med. rainfall and similarly for HL, MM, ML, & LL
Mean annual Temperature (MAT)	Cold with a MAT < 15°C (C) Moderate with MAT 15 – 16°C (M) Warm with a MAT > 16°C (W)	CC = both sites with temperatures < 15°C CM = one site with cold, the other mod. temps. and similarly for CW, MM, MW, & WW
Site Quality (SQ)	Site quality classes 1, 2 & 3 as defined by Loveday & Kassier, 1987 and allocated based on growth of genetic checks in each test	11 = both sites within SQ1 21 = one site in 1, the other in 2 and similarly for 31, 22, 23 & 33.
Climate index (CI)	Climate index was defined as the ratio of MAP To MAT. A CI defined as high if ratio > 70 (H), medium if 60 – 70 (M) and low if < 60 (L).	HH = both sites with CI's > 70 MH = one site with CI > 70, other 60 – 70. And similarly for LH, MM, LM & LL.

RESULTS AND DISCUSSION

The mean single-site, within-provenance heritability (h^2_b) increased with age from three to five years and then leveled off between five and eight years (Table 4). Mean h^2_b was 0.11 ± 0.01 for volume at age three, increasing to 0.18 ± 0.01 and 0.19 ± 0.01 at age five and eight respectively. Heritabilities were generally slightly higher for height and volume at all ages, than dbh. These estimates for heritability are similar to those reported elsewhere for the species in Zimbabwe (Barnes et al., 1992), although lower than those reported in the Mpumalanga province of South Africa recently, where individual tree heritabilities of 0.19 to 0.40 were reported (Sneddon and Verry, 1999).

In general, the estimates of type B genetic, provenance and aggregate family-provenance correlations follow a similar pattern to that described above in that they increase between three and five years and then remain at that level between five and eight (Table 4). There is also a small increase in the precision in which they are measured, as indicated by the decrease in the standard errors. Overall the average within provenance type B genetic correlations were 0.57 ± 0.04 for volume per tree at three years, going up to 0.76 ± 0.02 at eight years.

The type B provenance correlations were less precisely measured. This finding is similar to a previous study with *P. tecunumannii* (Hodge and Dvorak, 1999). However, in contrast to the findings in that latter study, the estimates for these type B provenance correlations were lower than the within provenance type B genetic correlations (Table 4). The estimates for *P. patula* ranged from 0.46 ± 0.05 at three years of age to 0.53 ± 0.05 at eight years. These results suggest that the provenances, are in fact less stable across environments than families within provenance.

Table 4: Mean single-site family within-provenance heritability estimates and type B genetic, provenance and aggregate family-provenance correlation estimates for volume at three, five and eight years of age in pairs of CAMCORE *P. patula* tests.

Parameter		db3	ht3	Vt3	db5	ht5	Vt5	db8	ht8	Vt8
h^2_b	N	33	33	33	29	29	29	24	24	24
	Range	0 - 0.27	0.03 - 0.31	0 - 0.32	0.07 - 0.42	0.05 - 0.39	0.05 - 0.38	0.08 - 0.39	0.07 - 0.43	0.11 - 0.43
	Mean	0.11	0.14	0.11	0.16	0.18	0.18	0.17	0.19	0.19
	Se	0.01	0.01	0.01	0.02	0.02	0.01	0.01	0.02	0.01
$r_{Bg(p)}$	N	64	64	64	60	60	60	51	51	51
	Range	0 - 1	0 - 1	0.05 - 1	0.30 - 1	0.54 - 1	0.28 - 1	0.26 - 1	0.49 - 1	0.39 - 1
	Mean	0.71	0.81	0.57	0.77	0.87	0.75	0.74	0.86	0.76
	Se	0.04	0.03	0.04	0.03	0.02	0.03	0.03	0.02	0.02
r_{Bp}	Range	0 - 1	0 - 1	0 - 1	0 - 1	0 - 1	0 - 1	0 - 1	0 - 1	0 - 1
	Mean	0.49	0.62	0.46	0.56	0.53	0.55	0.56	0.58	0.53
	Se	0.05	0.05	0.05	0.04	0.05	0.04	0.06	0.05	0.05
	Prov +									
r_{Bg}^1	Range			0 - 1			0 - 1			0.24 - 1
	Mean	*	*	0.53	*	*	0.68	*	*	0.67
	Fam variance Se			0.04			0.03			0.03

*Parameters not calculated.

¹Aggregate family-provenance type B correlations calculated using combined provenance and family variance.

The second method for estimating type B correlations combined the variance from both provenance and family origins. These estimates thus examine the overall variation attributable to the families, ignoring the provenance origins of the trees. These estimates have thus simply been termed the aggregate family-provenance type B correlations. The estimates of these genetic parameters, as would be expected, were intermediate between the within family type B genetic correlations and the type B provenance correlations (table 4). Overall, the estimates varied from 0.53 ± 0.04 for volume at three years to 0.67 ± 0.03 at eight years. A type B genetic correlation of 0.67 is the level at which the GxE variance represents 50% of the total additive variance and is the point when it is postulated the GxE variance may start to be a cause for some concern amongst tree breeders (Shelbourne, 1972). The latter result suggested that a more detailed look at the distribution of these type B genetic correlations across environmental variables within the region could be warranted. In previous studies relating the growth of *Pinus patula* to site factors, variables such as altitude, temperature, and water availability have been identified as important (Evans, 1974, Grey, 1979, Schutz, 1990 and Louw, 1995). Thus, as part of a preliminary study, the type B correlations were used to examine patterns of variation in five selected environmental variables (table 3).

Table 5: Mean type B aggregate family-provenance correlation estimates, combining family and provenance variation for volume, at three, five and eight years in pairs of *P. patula* provenance/progeny tests grouped within regional (REG) contrasts¹.

REG	Vt3			Vt5			Vt8		
Contrasts	N	Mean	Se	N	Mean	Se	N	Mean	Se
CC	1	0.60	0.31	1	0.69	0.25	1	0.79	0.18
CM	18	0.42	0.07	18	0.66	0.06	17	0.62	0.05
CN	6	0.75	0.13	6	0.64	0.10	6	0.70	0.07
MM	22	0.56	0.07	18	0.80	0.06	14	0.73	0.05
NM	16	0.50	0.08	16	0.56	0.06	14	0.63	0.05
NN	1	1.00	0.31	1	1.00	0.25	1	1.00	0.18
Tot/Mean	64	0.53		60	0.68		51	0.51	

¹CC = pairs both within the North-eastern Cape, CM = one site in the North-eastern Cape and one in Mpumalanga, CN = one site in the North-eastern Cape and one in Kwazulu-Natal, MM = pairs both within

Mpumalanga province, NM = one site in Kwazulu-Natal and one in Mpumalanga, NN = pairs both within Kwazulu-Natal.

Although, all of the factors showed some relationships with the GxE present, no one single variable tested, could be used to clearly explain the patterns of GxE present within the country (tables 5 – 9 and appendix 2 - 6). The type B correlations for each pair of sites were treated as individual observations and tested using analysis of variance (table 10). In all cases, some statistically significant differences were discernable but only at certain ages or with one of the three specific type B correlations estimated.

It is not entirely surprising that no clear patterns were discernable. None of the environmental variables on their own explained the growth patterns in any of the site-growth studies referred to above. It is likely that the genes determining tree growth are responding to a complex interaction of many environmental factors. Furthermore, the environmental factors themselves are likely to have been inaccurately measured. Some, like the mean annual rainfall and mean annual temperature are modeled using national data, and may in fact not reflect the true situation that those trees were growing on over that time period, on those sites. In addition, the type B correlations used, have high standard errors associated with the estimates and it is generally accepted that a large number of sites and tests are required to determine meaningful and repeatable patterns (Hodge, 1996). In this study, although 33 tests were available, this only equated to 7 sites and many of the 'environmental factor classes' were skewed (table 5 – 9 and appendix 2 – 6).

P. patula breeding and deployment in South Africa is now focused on achieving even greater gains in productivity from the forest landbase by deploying families and even clones. The result suggests that breeders will be trying to harness the potential for bigger genetic gains by narrowing the range of genotypes and providing effective genotype-site matching. It is suggested that future work should focus on looking at the environmental variables in greater detail, as well as integrating these factors more effectively. In addition, attempts will be made to define variables that more realistically reflect conditions on those sites in order to better classify sites into homogeneous groups or regions. The objective being the development of a model so that 'regions of uniformity' could be defined. Furthermore, this could also be more effectively achieved by incorporating a greater number of genetic tests into this study and broadening the range of sites tested. The potential to implement these suggestions is possible in South Africa and should be actively encouraged.

Table 6: Mean type B aggregate family-provenance correlation estimates, combining family and provenance variation for volume, at three, five and eight years in pairs of *P. patula* provenance/progeny tests, aggregated together according to mean annual precipitation(MAP) classes¹.

MAP Contrasts	Vt3			Vt5			Vt8		
	N	Mean	Se	N	Mean	Se	N	Mean	Se
HH	3	0.55	0.18	3	0.85	0.15	2	0.84	0.12
HL	19	0.49	0.07	17	0.59	0.06	15	0.57	0.05
HM	14	0.60	0.08	14	0.77	0.07	11	0.69	0.05
LL	9	0.75	0.10	9	0.67	0.08	9	0.75	0.06
ML	17	0.40	0.07	15	0.62	0.07	13	0.68	0.05
MM	2	0.57	0.22	2	0.95	0.18	2	0.87	0.18
Tot/Mean	64	0.53		60	0.68		51	0.67	

¹HH = pairs both categorized as high rainfall sites with rainfall exceeding 1000mm, HL = one site classed as high rainfall, the other as low, HM = one site classed as high rainfall, the other as medium, LL = pairs both categorized as low rainfall sites with rainfall less than 850mm, ML = one site classed as medium rainfall, the other as low, MM = pairs both categorized as low rainfall with rainfall between 850 and 1000mm.

Table 7: Mean type B aggregate family-provenance correlation estimates, combining family and provenance variation for volume, at three, five and eight years in pairs of *P.*

***patula* provenance/progeny tests, aggregated together according to mean annual temperature(MAT) classes¹.**

MAT Contrasts	Vt3			Vt5			Vt8		
	N	Mean	Se	N	Mean	Se	N	Mean	Se
CC	13	0.41	0.09	11	0.74	0.08	9	0.73	0.06
CM	14	0.59	0.08	14	0.59	0.07	13	0.69	0.05
CW	25	0.53	0.06	23	0.70	0.05	19	0.63	0.04
MM	1	1.00	0.32	1	1.00	0.26	1	1.00	0.18
MW	8	0.55	0.11	8	0.56	0.09	7	0.58	0.07
WW	3	0.55	0.18	3	0.85	0.15	2	0.84	0.13
Tot/Mean	64	0.53		60	0.68		51	0.67	

¹CC = pairs both categorized as cold sites with MAT's of less than 15°C, CM = one site classed as a cold site, the other as moderate, CW = one site classed as a cold site, the other as warm, MM = pairs both categorized as sites of moderate temperature between 15 and 16°C, MW = one site classed as a moderate site, the other as warm, WW = pairs both categorized as warm sites with MAT's above 16°C.

Table 8: Mean type B aggregate family-provenance correlation estimates, combining family and provenance variation for volume, at three, five and eight years in pairs of *P. patula* provenance/progeny tests, aggregated together according to site quality(SQ)¹ categories².

SQ Contrasts ¹	Vt3			Vt5			Vt8		
	N	Mean	Se	N	Mean	Se	N	Mean	Se
11	1	0.76	0.30	0	*	*	0	*	*
21	21	0.64	0.07	18	0.71	0.06	16	0.69	0.05
22	30	0.55	0.05	30	0.68	0.05	25	0.66	0.04
31	2	0.19	0.21	2	0.61	0.19	2	0.46	0.13
32	10	0.33	0.09	10	0.63	0.08	8	0.72	0.06
Tot/Mean	64	0.53		60	0.68		51	0.67	

¹Sites classed into three site quality classes(SQ) based on the growth of trees from the genetic tests in each test and compared to tables produced by Loveday and Kassier, 1987.

²11 = pairs of sites both classified as SQ 1, 21 = one site classed as a SQ 1, the other as SQ 2, 22 = pairs of sites both classified as SQ 2, 31 = one site classed as a SQ 3, the other as SQ 1, 32 = one site classed as SQ 3, the other as SQ 2, 33 = pairs of sites both classified as SQ 3.

Table 9: Mean type B aggregate family-provenance correlation estimates, combining family and provenance variation for volume, at three, five and eight years in pairs of *P. patula* provenance/progeny tests, aggregated together according to Climate Index(CI)¹ categories².

CI Contrasts	Vt3			Vt5			Vt8		
	N	Mean	Se	N	Mean	Se	N	Mean	Se
HH	3	0.55	0.18	3	0.85	0.15	2	0.84	0.12
LH	20	0.48	0.07	18	0.60	0.06	16	0.57	0.04
LL	9	0.75	0.10	9	0.67	0.09	9	0.75	0.06
LM	17	0.40	0.07	15	0.62	0.07	13	0.68	0.05
MH	13	0.62	0.08	13	0.76	0.07	10	0.70	0.06
MM	2	0.57	0.21	2	0.95	0.18	1	0.87	0.17
Tot/Mean	64	0.53		60	0.68		51	0.67	

¹Climate index is defined as the ratio of MAP to MAT.

²HH = pairs with both sites classed as having a high CI, LH = one site categorized as having a high CI, the other a low CI, LL = pairs with both sites classed sites as having a low CI, LM = one site categorized as having a moderate CI, the other a low CI, MH = one site categorized as having a high CI, the other as moderate, MM = pairs with both sites classed as having a high CI.

Table 10: Analysis of variance using type B genetic, provenance or aggregate family-provenance correlation parameter estimates to determine patterns of variation for various environmental variables used in models as fixed effects.

Environmental Parameters		Vt3			Vt5			Vt8		
		$r_{bg(p)}$	r_{bp}	$r_{bg(F)}$	$r_{bg(p)}$	r_{bp}	$r_{bg(F)}$	$r_{bg(p)}$	r_{bp}	$r_{bg(F)}$
Region	df	5	5	5	5	5	5	5	5	5
	Fprob	0.101	0.406	0.157	0.020*	0.747	0.108	0.120	0.085	0.217
MAP	df	5	5	5	5	5	5	5	5	5
	Fprob	0.076	0.173	0.122	0.185	0.481	0.159	0.237	0.001**	0.086
MAT	df	5	5	5	5	5	5	5	5	5
	Fprob	0.556	0.708	0.488	0.016*	0.577	0.209	0.112	0.002**	0.133
SQ	df	4	4	4	4	4	4	3	3	3
	Fprob	0.157	0.397	0.034*	0.617	0.440	0.854	0.205	0.591	0.351
CI	df	5	5	5	5	5	5	5	5	5
	Fprob	0.048*	0.170	0.107	0.267	0.506	0.219	0.348	0.001**	0.076

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Appendix 1: Estimated within provenance, single-site heritabilities for all growth traits assessed in 33 *P. patula* provenance/progeny tests in South Africa.

TESTID	Db3	Ht3	Vt3	Db5	Ht5	Vt5	Db8	Ht8	Vt8
200701L	0.03	0.06	0.04	0.14	0.17	0.16	0.19	0.13	0.17
200702D	0.19	0.24	0.23	0.23	0.27	0.28	0.22	0.14	0.25
200704C	0.20	0.10	0.18	*	*	*	*	*	*
200705L	0.19	0.15	0.16	0.30	0.18	0.28	0.22	0.12	0.25
200706E	0.18	0.29	0.22	0.20	0.38	0.30	0.14	0.22	0.23
200707D	0.03	0.14	0.05	0.10	0.26	0.16	0.13	0.07	0.16
200709B	0.16	0.22	0.18	*	*	*	*	*	*
200710B	0.04	0.11	0.05	*	*	*	*	*	*
201001A	0.07	0.05	0.05	0.12	0.11	0.13	0.15	0.14	0.17
201001B	0.08	0.07	0.11	0.13	0.14	0.17	0.21	0.17	0.24
201002A	0.06	0.09	0.06	0.10	0.11	0.10	0.10	0.11	0.12
201002B	0.13	0.31	0.10	0.42	0.39	0.38	0.39	0.38	0.43
201003A1	0.09	0.13	0.11	0.17	0.22	0.19	0.15	0.18	0.16
201003A2	0.16	0.30	0.11	0.26	0.36	0.28	0.20	0.43	0.26
201004A1	0.07	0.08	0.06	0.09	0.22	0.11	0.08	0.21	0.11
201004A2	0.09	0.08	0.10	0.10	0.11	0.15	0.13	0.12	0.15
201005E1	0.17	0.20	0.16	0.25	0.20	0.23	0.24	0.21	0.25
201005E2	0.03	0.06	0.05	0.13	0.05	0.12	0.21	0.10	0.21
201005F	0.13	0.15	0.17	0.22	0.21	0.24	*	*	*
201006B1	0.02	0.07	0.00	0.08	0.13	0.05	0.11	0.22	0.13
201006B2	0.11	0.03	0.10	0.12	0.09	0.13	0.14	0.23	0.16
201007B1	0.03	0.03	0.01	0.07	0.14	0.09	0.09	0.14	0.11
201007B2	0.11	0.14	0.08	0.15	0.12	0.16	0.16	0.22	0.18
201008A	0.06	0.11	0.06	0.13	0.11	0.10	*	*	*
201010C	0.00	0.05	0.00	*	*	*	*	*	*
201801H	0.08	0.08	0.09	0.09	0.14	0.13	*	*	*
201801J	0.12	0.12	0.16	0.12	0.16	0.16	0.10	0.10	0.14
201802E	0.27	0.30	0.32	0.28	0.25	0.29	0.21	0.23	0.24
201805K	0.15	0.19	0.20	0.20	0.16	0.22	0.17	0.13	0.19
201806D	0.14	0.28	0.20	0.16	0.25	0.22	0.15	0.36	0.23
201807A	0.24	0.16	0.24	0.12	0.13	0.13	0.11	0.11	0.12
201808B	0.05	0.05	0.05	0.05	0.07	0.05	*	*	*
201809A	0.09	0.11	0.10	0.11	0.17	0.15	*	*	*
Mean	0.11	0.14	0.11	0.16	0.18	0.18	0.17	0.19	0.19
Se*	0.01	0.01	0.01	0.02	0.02	0.02	0.01	0.02	0.01

*Simple empirical standard errors of the mean across all sites for each assessment.

Appendix 2a & b: Mean type B genetic (a) and provenance (b) correlation estimates, for volume, at three, five and eight years in pairs of *P. patula* provenance/progeny tests grouped within regional(REG) contrasts¹.

a) rBg's

REG Contrasts	Vt3			Vt5			Vt8		
	N	Mean	Se	N	Mean	Se	N	Mean	Se
CC	1	0.43	0.33	1	0.68	0.20	1	0.77	0.16
CM	18	0.42	0.08	18	0.79	0.05	17	0.76	0.04
CN	6	0.80	0.13	6	0.67	0.08	6	0.68	0.07
MM	22	0.64	0.07	18	0.85	0.05	14	0.84	0.04
NM	16	0.55	0.08	16	0.62	0.05	14	0.70	0.04
NN	1	1.00	0.33	1	1.00	0.20	1	1.00	0.16
Tot/Mean	64	0.57		60	0.75		51	0.76	

b) rBp's

REG Contrasts	Vt3			Vt5			Vt8		
	N	Mean	Se	N	Mean	Se	N	Mean	Se
CC	1	1.00	0.40	1	0.68	0.34	1	0.86	0.35
CM	18	0.38	0.09	18	0.49	0.08	17	0.50	0.09
CN	6	0.67	0.16	6	0.62	0.14	6	0.86	0.14
MM	22	0.43	0.09	18	0.58	0.08	14	0.39	0.10
NM	16	0.45	0.10	16	0.54	0.08	14	0.49	0.09
NN	1	0.84	0.40	1	0.98	0.34	1	0.96	0.35
Tot/Mean	64	0.46		60	0.55		51	0.53	

¹CC = pairs both within the North-eastern Cape, CM = one site in the North-eastern Cape and one in Mpumalanga, CN = one site in the North-eastern Cape and one in Kwazulu-Natal, MM = pairs both within Mpumalanga province, NM = one site in Kwazulu-Natal and one in Mpumalanga, NN = pairs both within Kwazulu-Natal.

Appendix 3a & b: Mean type B genetic (a) and provenance (b) correlation estimates for volume, at three, five and eight years in pairs of *P. patula* provenance/progeny tests, aggregated together according to mean annual precipitation(MAP) classes¹.

a) rBg's

MAP Contrasts ¹	Vt3			Vt5			Vt8		
	N	Mean	Se	N	Mean	Se	N	Mean	Se
HH	3	0.65	0.19	3	0.89	0.12	2	0.93	0.12
HL	19	0.52	0.07	17	0.72	0.05	15	0.72	0.04
HM	14	0.69	0.09	14	0.85	0.06	11	0.82	0.05
LL	9	0.75	0.11	9	0.69	0.07	9	0.73	0.06
ML	17	0.40	0.08	15	0.69	0.05	13	0.74	0.05
MM	2	0.82	0.23	2	0.92	0.15	2	0.97	0.17
Tot/Mean	64	0.57		60	0.75		51	0.76	

b) rBp's

MAP Contrasts ¹	Vt3			Vt5			Vt8		
	N	Mean	Se	N	Mean	Se	N	Mean	Se
HH	3	0.29	0.23	3	0.64	0.19	2	0.45	0.22
HL	19	0.47	0.09	17	0.45	0.08	15	0.33	0.08
HM	14	0.44	0.11	14	0.53	0.09	11	0.36	0.09

LL	9	0.76	0.13	9	0.68	0.11	9	0.89	0.10
ML	17	0.36	0.10	15	0.56	0.09	13	0.67	0.09
MM	2	0.18	0.28	2	0.82	0.24	2	0.30	0.31
Tot/Mean	64	0.46		60	0.55		51	0.53	

¹HH = pairs both categorized as high rainfall sites with rainfall exceeding 1000mm, HL = one site classed as high rainfall, the other as low, HM = one site classed as high rainfall, the other as medium, LL = pairs both categorized as low rainfall sites with rainfall less than 850mm, ML = one site classed as medium rainfall, the other as low, MM = pairs both categorized as low rainfall with rainfall between 850 and 1000mm.

Appendix 4a & b: Mean type B genetic (a) and provenance (b) correlation estimates for volume, at three, five and eight years in pairs of *P. patula* provenance/progeny tests, aggregated together according to mean annual temperature(MAT) classes¹.

a) rBg's

MAT Contrasts ¹	Vt3			Vt5			Vt8		
	N	Mean	Se	N	Mean	Se	N	Mean	Se
CC	13	0.45	0.09	3	0.81	0.06	2	0.81	0.05
CM	14	0.60	0.09	17	0.61	0.05	15	0.68	0.04
CW	25	0.58	0.07	14	0.82	0.04	11	0.78	0.04
MM	1	1.00	0.34	9	1.00	0.20	9	1.00	0.16
MW	8	0.64	0.12	15	0.67	0.07	13	0.71	0.06
WW	3	0.65	0.20	2	0.89	0.11	2	0.93	0.11
Tot/Mean	64	0.57		60	0.75		51	0.76	

b) rBp's

MAT Contrasts ¹	Vt3			Vt5			Vt8		
	N	Mean	Se	N	Mean	Se	N	Mean	Se
CC	13	0.37	0.11	3	0.62	0.10	2	0.64	0.11
CM	14	0.56	0.11	17	0.60	0.09	15	0.80	0.09
CW	25	0.45	0.08	14	0.48	0.07	11	0.38	0.07
MM	1	0.84	0.41	9	0.98	0.33	9	0.96	0.32
MW	8	0.50	0.14	15	0.50	0.12	13	0.26	0.12
WW	3	0.29	0.24	2	0.64	0.19	2	0.45	0.22
Tot/Mean	64	0.46		60	0.55		51	0.53	

¹CC = pairs both categorized as cold sites with MAT's of less than 15°C, CM = one site classed as a cold site, the other as moderate, CW = one site classed as a cold site, the other as warm, MM = pairs both categorized as sites of moderate temperature between 15 and 16°C, MW = one site classed as a moderate site, the other as warm, WW = pairs both categorized as warm sites with MAT's above 16°C.

Appendix 5a & b: Mean type B genetic (a) and provenance (b) correlation estimates for volume, at three, five and eight years in pairs of *P. patula* provenance/progeny tests, aggregated together according to site quality(SQ)¹ categories².

a) rBg's

SQ Contrasts ¹	Vt3			Vt5			Vt8		
	N	Mean	Se	N	Mean	Se	N	Mean	Se
11	1	0.46	0.33	0	*	*	0	*	*
21	20	0.65	0.07	17	0.72	0.05	15	0.72	0.04
22	30	0.61	0.06	30	0.79	0.04	25	0.76	0.03
31	2	0.24	0.23	2	0.65	0.15	2	0.63	0.12
32	11	0.39	0.10	11	0.72	0.06	9	0.85	0.06
Tot/Mean	64	0.57		60	0.75		51	0.76	

b) rBp's

MAT Contrasts ¹	Vt3			Vt5			Vt8		
	N	Mean	Se	N	Mean	Se	N	Mean	Se
11	1	0.61	0.40	0	*	*	0	*	*
21	20	0.59	0.09	17	0.66	0.08	15	0.58	0.10
22	30	0.40	0.07	31	0.52	0.06	25	0.55	0.07
31	2	0.16	0.28	2	0.48	0.23	2	0.23	0.26
32	11	0.42	0.12	11	0.48	0.10	9	0.46	0.12
Tot/Mean	64	0.46		60	0.55		51	0.53	

¹Sites classed into three site quality classes(SQ) based on the growth of trees from the genetic tests in each test and compared to tables produced by Loveday and Kassier, 1987.

²11 = pairs of sites both classified as SQ 1, 21 = one site classed as a SQ 1, the other as SQ 2, 22 = pairs of sites both classified as SQ 2, 31 = one site classed as a SQ 3, the other as SQ 1, 32 = one site classed as SQ 3, the other as SQ 2, 33 = pairs of sites both classified as SQ 3.

Appendix 6a & b: Mean type B genetic (a) and provenance (b) correlation estimates for volume, at three, five and eight years in pairs of *P. patula* provenance/progeny tests, aggregated together according to Climate Index(CI)¹ categories ²

a) rBg's

CI Contrasts ¹	Vt3			Vt5			Vt8		
	N	Mean	Se	N	Mean	Se	N	Mean	Se
HH	3	0.65	0.19	3	0.89	0.12	2	0.93	0.12
LH	20	0.51	0.07	18	0.74	0.05	16	0.73	0.04
LL	9	0.75	0.11	9	0.69	0.07	9	0.73	0.06
LM	17	0.40	0.08	15	0.69	0.05	13	0.74	0.05
MH	13	0.72	0.09	13	0.83	0.06	10	0.81	0.05
MM	2	0.81	0.23	2	0.92	0.15	1	0.97	0.17
Tot/Mean	64	0.57		60	0.75		51	0.76	

b) rBp's

CI Contrasts ¹	Vt3			Vt5			Vt8		
	N	Mean	Se	N	Mean	Se	N	Mean	Se
HH	3	0.29	0.23	3	0.64	0.19	2	0.45	0.22
LH	20	0.48	0.09	18	0.46	0.08	16	0.32	0.08
LL	9	0.76	0.13	9	0.68	0.11	9	0.89	0.10
LM	17	0.36	0.10	15	0.56	0.09	13	0.67	0.09
MH	13	0.43	0.11	13	0.52	0.09	10	0.39	0.10
MM	2	0.18	0.28	2	0.83	0.24	1	0.30	0.31
Tot/Mean	64	0.46		60	0.55		51	0.53	

¹Climate index defined as the ratio of MAP to MAT.

²HH = pairs with both sites classed as having a high CI, LH = one site categorized as having a high CI, the other a low CI, LL = pairs with both sites classed sites as having a low CI, LM = one site categorized as having a moderate CI, the other a low CI, MH = one site categorized as having a high CI, the other as moderate, MM = pairs with both sites classed as having a high CI.

CHAPTER 4 – AN ASSESSMENT OF THE EXTENT AND AMOUNT OF G_xE IN SOUTHERN AFRICA USING THE TYPE B GENETIC CORRELATION METHOD

Chapter Summary

4.1 Introduction

4.2 Analysis of all CAMCORE provenance / progeny trials in Southern Africa

4.3 Analysis of all FAO provenance trials in Southern Africa

4.4 Analysis of an ICFR progeny trial series in Southern Africa

4.5 Analysis of a Sappi progeny trial series in Southern Africa

4.6 General Discussion and Conclusions

4.1 Introduction

4.1.1 In the previous chapter the extent of GxE in the CAMCORE trials was examined in general terms. Genetic parameters such heritabilities and Type B genetic correlations were calculated and reported and some general conclusions were reached. Amongst these, was the finding that the genetic parameters tend to increase from 3 to 5 years and then remain relatively constant from 5 to 8 years in *P. patula*. In addition, other studies have indicated that the genetic correlations for growth characteristics between five and eight years are high ((Barnes et al., 1992;Hodge, 2000). These latter two findings suggest that the 5 - year assessments can be considered in any further work. This also represents the age where data is most frequently available in a majority of the trials.

4.1.2 The objective of this chapter is to consider and quantify the amount of interaction present within the sub-region. All possible trials are considered and analysed to determine the overall precision and where possible the Type B genetic correlations between these trials.

4.2 Analysis of all CAMCORE provenance/progeny trials in Southern Africa

4.2.1 General introduction

4.2.1.1 The background to these trials has been outlined in the previous chapter. Further work on these trials, using the five-year data where possible, will focus on quantifying the amount of GxE present in these trials. All possible trials with common CAMCORE material present will be utilised. Five additional trials were available for this work (Table 4.2.1 and see Appendix 1 for more details).

4.2.2 Method – assessments, data preparation and analysis

An outline of the general methodology used in each of the CAMCORE series is presented below.

4.2.2.1 Trial assessment and data preparation

Details of this can be found in the previous chapter. Tree volumes were calculated in two ways. A volume index as in chapter 3, was calculated using height and DBH in the formula: Volume = 0.00003 (DBH² * height) for juvenile trees (Ladrach and Mazuera, 1978). In the second approach, an equation based on the Schumacher and Hall Model, developed for South African

grown *P. patula* was used (Bredankamp and Loveday, 1984). The equation and coefficients are given below:-

$$\text{Log}_{10} V = b_0 + b_1 \log_{10} (D + d) + b_2 \log_{10} H$$

Where:	\log_{10}	=	common logarithm to the base 10
	V	=	stem volume (m ³), to 75mm tip diameter
	D	=	breast height diameter (mm)
	d	=	80 (a correction factor (mm))
	H	=	tree height (m)
	b ₀	=	- 8.28929
	b ₁	=	2.43963
	b ₂	=	1.32537

There was little difference between the genetic parameters calculated using either volume equation, and only results using the latter equation are reported here. Height to diameter ratios were calculated by dividing the height (in meters) by the dbh (converted to meters) to obtain a unitless ratio.

Table 4.2.1: Summary information for CAMCORE *P. patula* tests in South Africa, additional to those used in chapter 3, and included in Analyses.

Test code	Region	Location	Lat.	Long.	Age (yrs)	Nr. Family(prov) Representation**
20-07-08C	Mpumalanga	Helvetia A39	25°34'S	30°22'E	7	PM(7), EC(10), LE(9), CM(10), CB(8), LC(10), CON(4)
20-07-15E		Hlelo	26°57'S	30°41'E	3	SH(37), ACX(10), CON(11)
PV34B1		Magsleigh	25°12'S	30°46'E	8	PM(18), IR(11), CO(19), PM(18), EM(15), ET(8), IX(10), CON(3)
PV34B2		Magsleigh	25°12'S	30°46'E	8	CC(22), PA(22), ZA(8), LLC(13), CON(4)
20-10-15I		Tweefontein B78	25°03'S	30°45'E	3	SH(34), ACX(8), CON(11)
20-18-10E	KZN	Tetworth A4a			5	
PV34C1		Goodhope	29°55'S	29°42'E	8	PM(8), IR(5), CO(13), CON(4)
PV34C2		Goodhope	29°55'S	29°42'E	8	CC(19), TL(1), PA(13), ZA(5), LLC(9), CON(4)
R203	Swaziland	Usutu S1	26°22'S	30°55'E	3	SH(23), CON(12)

**CON represents other controls.

4.2.2.2 Single site analysis

For each test, single-site heritability estimates were calculated. The methodology for the within provenance estimates is described in chapter 3.

A second method used to estimate single-site heritabilities was to ignore the provenance effect and calculate single-site heritabilities, which effectively pools the genetic effect of both family and provenance. In this case the linear model utilized is outlined below:

$$Y_{ijklm} = \mu_i + B_j + F_k + B^*F_{jk} + \epsilon_{ijkl}$$

where, Y_{ijkl} phenotypic observation for the $ijkl^{\text{th}}$ tree,

μ_i = mean in the i^{th} test,

B_j = fixed effect of the j^{th} block,

F_k = random effect of the k^{th} family, $E[F_k] = 0$, $\text{Var}[F_k] = \sigma_F^2$,

B^*F_{jk} = random effect of the jk^{th} row-plot, i.e. the interaction of the j^{th} block with the k^{th} family, $E[B^*F_{jk}] = 0$, $\text{Var}[B^*F_{jk}] = \sigma_{b^*f}^2$,

ϵ_{ijkl} = random error term associated with the $ijkl^{\text{th}}$ tree, $E[\epsilon_{ijkl}] = 0$, $\text{Var}[\epsilon_{ijkl}] = \sigma_e^2$.

Variance components for all traits were estimated using the PROC MIXED procedure in SAS.

The phenotypic variance (σ_T^2) was estimated as follows:-

$$\sigma_T^2 = \sigma_F^2 + \sigma_{b^*f}^2 + \sigma_e^2$$

Single-site heritability estimates within provenance (h_w^2) were estimated for all growth traits assessed, and for all tests separately, using the formula:

$$h_w^2 = \frac{3 \sigma_F^2}{\sigma_T^2}$$

A coefficient of 3 instead of 4 was again used when multiplying by the family variance to give an estimate of the additive genetic variance. The reasons for this are identical to those outlined in chapter 3.

4.2.2.3 Paired and overall across site analysis

Paired site analyses were conducted for all pairs of tests as outlined in chapter 3. In these analyses all genetic checks were removed and the data was not standardized. Initially no restrictions were placed on any pair combination, even though in some cases very few families were common to some test pairs (table 3.3). However, any pairs that did not have at least 20 families in common and where the single-site, within provenance heritability (h_w^2) was less than 0.05 for either of the pair of tests, were noted. These analyses were conducted in order to quantify the level of genotype x environment interaction (GxE) present both among families and provenances.

As noted previously the analyses were conducted in two different ways. In the first method, both the provenance and family effects were identified and kept separate, with the family effect being within provenance; whereas, in the second approach the provenance effect was ignored and thus all variation due to genetic effects at both provenance and family level was pooled.

In addition to the above paired-site analyses, an across-site analyses was done using all tests for the trial series together. The objective was to determine the overall significance of the GxE variance to the genetic variance and compare to the individual paired site Type B genetic correlation estimates. These analyses were only carried out for the volume.

4.2.3 Analysis of the 01 and 04 series of trials

4.2.3.1 Introduction

This trial series tested three sources of *P. patula* var. *patula* collected from locations in Mexico. These provenances include Potrero de Monroy, Ingenio del Rosario and Corralitla. Two of these provenances, Potrero de Monroy and Corralitla have been reported as being amongst the most productive of the provenances tested, both in South Africa and Brazil (Dvorak et al., 2000).

4.2.3.2 Trial composition

The three provenances of *P. patula* are represented by approximately 10 – 30 half-sib families each. Details of the composition of each trial is presented in Appendix 3. A matrix of the number of common treatments present in each of a pair of trials is presented in table 4.2.2.

4.2.3.3 Trial design, management and site details

This series contains 10 tests. The sites ranged from Tweefontein in the north, in Mpumalanga province, through KwaZulu-Natal (KZN), to Ugie in the South in the Eastern Cape province. This range spans much of the summer rainfall area of South Africa that has been planted up with commercial, exotic plantations. Some details of the exact location and basic climatic data are presented in appendix 1 and table 4.2.1 above. The trial design for these CAMCORE tests has been described previously and was the same at all locations, with the exception of the two trials PV34B1 & PV34C1. In these latter 2 tests, only 4 replications of 6 tree line plots were planted. All trees in all tests were planted at a spacing between trees of 3m x 3m.

4.2.3.4 Single site analyses

Single site heritability estimates for growth characteristics at 5 & 8 years respectively are presented in tables 4.2.3 & 4.2.4, using the two different methods outlined in section 4.2.2.3 and chapter 3.

4.2.3.5 Paired and multiple site analyses

The Type B genetic, provenance and aggregate family-provenance correlation estimates for age 5 and age 8 are presented on tables 4.2.5 and 4.2.6 respectively. The latter estimates are presented for age 8 years for those pair wise comparisons with the 2 'additional' trials (PV34B1 & PV34C1) where no 5-year assessments were available.

The proportions of the variance components for the provenance and family effects and their interactions at both 5 and 8-year volume, when analyzed across all tests in the series, are presented in table 4.2.7.

Table 4.2.2: Number of individual OP families common to each pair of trials in all eight tests of the CAMCORE 01 & 04 series*.

	20-10-01A	20-10-01B	20-18-01H	20-07-01L	20-18-01J	20-10-04A1	20-07-04C	20-10-04A2	34B1	34C1
20-10-01A	50	46	49	47	46	11	11	9	33	25
20-10-01B	*	46	45	45	45	11	11	9	33	25
20-18-01H	*	*	51	46	45	11	12	9	32	24
20-07-01L	*	*	*	47	44	11	11	9	33	25
20-18-01J	*	*	*	*	46	10	10	9	32	25
20-10-04A1	*	*	*	*	*	32	32	30	19	4
20-07-04C	*	*	*	*	*	*	35	30	19	4
20-10-04A2	*	*	*	*	*	*	*	30	18	4
34B1	*	*	*	*	*	*	*	*	48	26
34C1	*	*	*	*	*	*	*	*	*	26

*Shaded cells refer to pairs with less than 20 OP families in common.

Table 4.2.3: Single-site within-provenance (h^2_w) and aggregate family-provenance (h^2_a) heritability estimates for diameter at breast height (D5), total tree height (H5), height / diameter ratio (HD5) and volume per tree (V5) at 5 years of age in CAMCORE trial series 01 & 04.

Trait	Parameter	Test								Mean	Range
		20-10-01A	20-10-01B	20-18-01H	20-07-01L	20-18-01J	20-10-04A1	20-07-04C	20-10-04A2		
D5	h^2_w	0.12	0.12	0.09	0.14	0.12	0.09	0.19	0.10	0.12	0.09 – 0.19
	h^2_a	0.18	0.17	0.20	0.18	0.12	0.11	0.21	0.16	0.17	0.11 – 0.21
H5	h^2_w	0.12	0.13	0.14	0.18	0.15	0.21	0.18	0.12	0.15	0.12 – 0.21
	h^2_a	0.17	0.17	0.43	0.26	0.18	0.28	0.20	0.27	0.24	0.17 – 0.43
HD5	h^2_w	0.09	0.04	0.04	0.13	0.10	0.07	0.10	0.06	0.08	0.04 – 0.13
	h^2_a	0.10	0.06	0.05	0.13	0.11	0.15	0.12	0.19	0.11	0.05 – 0.19
V5	h^2_w	0.13	0.16	0.14	0.17	0.16	0.12	0.22	0.17	0.16	0.12 – 0.22
	h^2_a	0.18	0.22	0.34	0.23	0.17	0.15	0.25	0.22	0.22	0.15 – 0.34

Table 4.2.4: Single-site within-provenance (h^2_w) and aggregate family-provenance (h^2_a) heritability estimates for diameter at breast height (D8), total tree height (H8), height / diameter ratio (HD8) and volume per tree (V8) at 8 years of age in CAMCORE trial series 01 & 04.

Trait	Parameter	Test								Mean	Range
		20-10-01A	20-10-01B	20-07-01L	20-18-01J	20-10-04A1	20-10-04A2	34B1	34C1		
D8	h^2_w	0.15	0.20	0.19	0.10	0.07	0.12	0.19	0.27	0.16	0.07 – 0.27
	h^2_a	0.18	0.25	0.21	0.13	0.09	0.19	0.25	0.35	0.21	0.09 – 0.35
H8	h^2_w	0.14	0.17	0.13	0.10	0.20	0.12	0.13	0.23	0.15	0.10 – 0.23
	h^2_a	0.18	0.20	0.16	0.20	0.24	0.31	0.17	0.51	0.24	0.16 – 0.51
HD8	h^2_w	0.08	0.14	0.19	0.08	0.04	0.09	0.11	0.00	0.09	0.00 – 0.19
	h^2_a	0.09	0.16	0.19	0.08	0.09	0.26	0.13	0.00	0.12	0.00 – 0.26
V8	h^2_w	0.17	0.24	0.17	0.14	0.12	0.15	0.19	0.35	0.19	0.12 – 0.35
	h^2_a	0.21	0.30	0.20	0.21	0.14	0.21	0.24	0.51	0.25	0.14 – 0.51

Table 4.2.5: Type B genetic, provenance and aggregate family-provenance correlation estimates for all pairs of tests for diameter at breast height (D5), total tree height (H5), height / diameter ratio (HD5) and volume per tree (V5) at 5 years of age in CAMCORE trial series 01 & 04.

Paired sites		D5			H5			HD5			V5		
Test1	Test2	R_{Bg}	R_{bp}	R_{Bg}^*	R_{Bg}	R_{bp}	R_{Bg}^*	R_{Bg}	R_{bp}	R_{Bg}^*	R_{Bg}	R_{bp}	R_{Bg}^*
20-10-01a	20-10-01b	0.73	1.00	0.81	0.76	0.67	0.74	0.50	1.00	0.63	0.79	1.00	0.83
20-10-01a	20-18-01h	0.60	0.23	0.49	0.75	0.04	0.46	0.37	1.00	0.43	0.69	0.07	0.51
20-10-01a	20-07-01l	0.67	0.91	0.71	0.79	0.55	0.72	0.58	1.00	0.64	0.79	0.67	0.75
20-10-01a	20-18-01j	0.52	0.42	0.50	0.45	0.00	0.33	0.84	1.00	0.86	0.50	0.08	0.45
20-10-01b	20-18-01h	1.00	0.83	0.96	1.00	0.62	0.80	0.82	0.97	0.85	1.00	0.87	0.96
20-10-01b	20-07-01l	0.67	1.00	0.82	0.87	1.00	0.96	0.74	1.00	0.80	0.73	1.00	0.86
20-10-01b	20-18-01j	0.96	0.97	0.95	0.99	1.00	1.00	0.89	0.70	0.85	0.94	1.00	0.95
20-18-01h	20-07-01l	0.83	0.89	0.84	0.75	0.81	0.78	1.00	1.00	1.00	0.71	1.00	0.83
20-18-01h	20-18-01j	1.00	0.40	0.83	1.00	0.60	0.80	0.64	1.00	0.68	1.00	0.57	0.83
20-07-01l	20-18-01j	0.35	1.00	0.44	0.56	0.93	0.65	0.32	1.00	0.37	0.44	0.86	0.52
20-10-04a1	20-10-04c	0.66	1.00	0.75	0.58	1.00	0.66	0.86	0.72	0.77	0.58	1.00	0.65
20-10-04a1	20-10-04a2	0.99	1.00	1.00	0.74	1.00	0.93	0.53	1.00	0.82	0.77	1.00	0.89
20-10-04a2	20-10-04c	0.79	1.00	0.23	0.54	0.98	0.65	0.65	1.00	0.84	0.65	1.00	0.71
	Mean	0.75	0.82	0.72	0.75	0.71	0.73	0.67	0.95	0.73	0.74	0.78	0.75
	Minimum	0.35	0.23	0.23	0.45	0.00	0.33	0.32	0.70	0.37	0.44	0.07	0.45
	Maximum	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.96

*Aggregate family – provenance type B genetic correlation

Table 4.2.6: Type B genetic, provenance and aggregate family-provenance correlation estimates for all those comparisons between the CAMCORE trials and the 2 ‘additional’ tests (PV34B1 & PV34C1)) for diameter at breast height (D8), total tree height (H8), height / diameter ratio (HD8) and volume per tree (V8) at 8 years of age in CAMCORE trial series 01 & 04.

Paired sites		D8			H8			HD8			V8		
Test1	Test2	R _{Bg}	R _{bp}	R _{Bg} *	R _{Bg}	R _{bp}	R _{Bg} *	R _{Bg}	R _{bp}	R _{Bg} *	R _{Bg}	R _{bp}	R _{Bg} *
20-10-01A	PV34B1	1.00	1.00	1.00	1.00	1.00	1.00	0.93	0.00	0.85	1.00	1.00	1.00
20-10-01A	PV34C1	0.57	0.21	0.36	0.57	0.00	0.10	1.00	*	1.00	0.45	0.05	0.20
20-10-01B	PV34B1	0.91	0.00	0.80	0.48	0.00	0.40	1.00	0.00	1.00	0.90	0.00	0.75
20-10-01B	PV34C1	0.77	1.00	0.85	0.87	0.73	0.88	0.67	*	0.79	0.74	0.97	0.80
20-18-01J	PV34B1	0.74	0.00	0.58	0.78	0.15	0.44	0.85	0.49	0.86	0.67	0.00	0.43
20-18-01J	PV34C1	0.81	0.98	0.87	0.93	1.00	1.00	0.64	1.00	0.64	0.74	0.88	0.79
20-07-01L	PV34B1	0.79	0.00	0.57	0.72	0.00	0.73	0.47	0.00	0.38	0.91	0.00	0.63
20-07-01L	PV34C1	0.51	1.00	0.61	0.39	0.83	0.62	0.78	*	0.78	0.47	1.00	0.59
PV34C1	PV34B1	0.98	0.00	0.41	0.84	0.04	0.30	1.00	0.64	1.00	0.78	0.00	0.23
	Mean	0.79	0.46	0.67	0.73	0.42	0.61	0.82	0.36	0.81	0.74	0.43	0.60
	Minimum	0.51	0.00	0.36	0.39	0.00	0.10	0.47	0.00	0.38	0.45	0.00	0.20
	Maximum	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

*Aggregate family – provenance type B genetic correlation

Table 4.2.7: The proportions of the variance components for the provenance, family with provenance and aggregate family/provenance family effects and their interactions at 5 years for volume in CAMCORE trial series 01 & 04, analyzed across all tests.

Parameters estimated	Proportions	5-year data
Fam(Prov) / Fam(Prov) + Fam x Env.**	$\sigma_{f(p)}^2 / \sigma_{f(p)}^2 + \sigma_{fe}^2$	0.73
Prov / Prov + Prov x Env.*	$\sigma_p^2 / \sigma_p^2 + \sigma_{pe}^2$	0.51
agg. Fam / agg. Fam + agg.Fam x Env.***	$\sigma_f^2 / \sigma_f^2 + \sigma_{fe}^2$	0.76
Prov x Env. / Prov	$\sigma_{pe}^2 / \sigma_p^2$	0.96
Fam(Prov) x Env. / Fam(Prov)	$\sigma_{fe}^2 / \sigma_{f(p)}^2$	0.37
agg. Fam x Env. / agg. Fam	$\sigma_{fe}^2 / \sigma_f^2$	0.32

*Refers to the ratio of provenance variance over the combined provenance and provenance x environment variance – this is equivalent to a Type B provenance correlation from a paired site analysis.

**Refers to the family within provenance ratio of family variance over the combined family and family x environment variance – this is equivalent to a Type B genetic correlation from a paired site analysis.

***Refers to the aggregate family-provenance ratio of genetic variance over the combined genetic and genetic x environment variance – this is equivalent to a aggregate Type B genetic correlation from a paired site analysis.

4.2.3.6 Discussion

Single-site within-provenance heritability estimates calculated for all tests generally ranged between 0.10 and 0.35 for all traits at both 5 and 8 years of age (Table 4.2.3 & 4.2.4). A single-site heritability estimate of at least 0.05 for both pairs of tests was considered to be a minimum requirement necessary to calculate Type B genetic correlations (Hodge and Dvorak, 1999). The estimates for volume were, on average, between 0.15 and 0.20, with little increase between the

ages of 5 and 8 years. There did not appear to be any clear trends between single-site heritability estimates within provenance (h^2_w) amongst the other traits assessed. The only exception to the above was for the height / diameter ratios, where in some trials no differences between OP families were apparent. This varied for this latter trait considerably, however, with some tests exhibiting clear genetic differences with a maximum estimated within-provenance heritability estimate of 0.19 (Table 4.2.4).

Estimates of within-provenance heritability for volume per tree (V) as calculated using volume equations derived from work on South African grown *P. patula* (Bredankamp and Loveday, 1984) did not differ appreciably from volumes calculated using a simple volume index. Thus only the former were reported here and in all other subsequent sections. As expected, the single-site aggregate family-provenance heritability estimates were generally much higher than the former within-provenance heritability estimates. Indeed, some of these were extremely high which reflects upon the marked differences between provenance performance in many tests.

The Type B provenance correlations (r_{Bp}) between pairs of tests were generally marginally higher (around 0.80) than for the family-within-provenance Type B genetic correlations (r_{Bg}) averaged at 0.75, (Table 4.2.5) with the exception of those trials paired with the 2 additional trials PV34B1 and PV34C1 (Table 4.2.6). In other words, the provenance by site interaction is slightly lower than the family within provenance by site interaction. This is not the case when looking at the CAMCORE tests in South Africa as a whole (see chapter 3). The lower levels of GxE at the provenance level may be a reflection of the provenances sampled. The 3 provenances included in this trial series all originate from the central area of the distribution of the species in Mexico. They are thus geographically speaking relatively close together. Nevertheless, distinct overall differences in productivity between these three provenances in South Africa have been reported (Dvorak et al., 2000). The lower Type B provenance correlations observed for the 8 year comparisons between all trials and the 2 additional trials, PV34B1 and PV34C1, may be due to two factors. The experimental design of these latter 2 tests did not include the blocking of provenance within replications. Competition between families from different provenances in line plots growing alongside each other may distort and indeed accentuate the provenance differences. It may also be due to the 5 and 8 year age differences although this was not apparent as an overall trend amongst the other CAMCORE tests in this series.

The overall average aggregate provenance-family Type B genetic correlations were around 0.65 to 0.75 for volume with similar trends amongst the other growth traits assessed (Table 4.2.5 & 4.2.6). Again the average for the 8 year comparisons between all tests and the 2 additional tests

(PV34B1 & C1) are lower for reasons discussed previously. The height to diameter ratios (HD) exhibits levels of GxE similar to other growth traits.

The overall ratio of GxE variance to genetic variance for volume at 5 years varies between 0.96 for provenance to 0.32 for the aggregate provenance-family estimates (Table 7.2.7). The estimates of the ratios of genetic to genetic plus GxE variances when analysed across all sites is not always comparable to the means of the paired-site Type B correlation estimates (see Table 4.2.5 & 4.2.7). The discrepancy is large for provenance, and may relate to the fact that the analyses were performed with unstandardised data, and some paired-site estimates were not included in the means given in table 4.2.5 because they had less than the minimum number of common families.

4.2.4 Analysis of the 02 and 03 series of trials

4.2.4.1 Introduction

This trial series tested 5 sources of *P. patula* collected from locations in Mexico. These included the provenances of Potrero de Monroy, Santa Maria Papalo, Ixtlan, El Tlacuache and El Manzanal. The latter 4 are found in the Southern Mexican State of Oaxaca and have been identified as belonging to *P. patula* var. *longipedunculata* whilst Potrero de Monroy is found to the north in the state of Veracruz and is regarded as being of the variety *P. patula* var. *patula*.

4.2.4.2 Trial composition

Details of the composition of each trial are presented in appendix 4. A matrix of the number of common treatments in each of a pair of trials is presented in table 4.2.8.

4.2.4.3 Trial design, management and site details

This series contain 7 tests. The sites ranged from Tweefontein in the north, in Mpumalanga province, through KwaZulu-Natal (KZN), to Ugie in the South in the Eastern Cape province. This range spans much of the summer rainfall area of South Africa that has been planted up with commercial, exotic plantations. Some further details of the exact location and basic climatic data for each of the tests are presented in appendix 1 and table 4.2.1 in this chapter.

The trial design for these CAMCORE tests has been described previously and was the same at all locations, with the exception of the 1 trial - PV34B1. In this latter test only 4 replications of 6

tree line plots were planted. All trees in all tests were planted at a spacing between trees of 3m x 3m.

Table 4.2.8: Number of individual OP families common to each pair of trials in all 7 tests of the CAMCORE 02 & 03 series.

	201002A	201002B	200702D	201802E	201003A1	201003A2	34B1
201002A	57	49	56	55	17	17	26
201002B	*	57	49	49	17	17	26
200702D	*	*	56	54	17	17	26
201802E	*	*	*	56	17	17	26
201003A1	*	*	*	*	49	39	14
201003A2	*	*	*	*	*	40	13
34B1	*	*	*	*	*	*	51

Shaded cells refer to pairs with less than 20 OP families in common.

4.2.4.4 Single-site analyses

Single-site heritability estimates for growth characteristics at 5 & 8 years respectively, are presented in tables 4.2.9 & 4.2.10, using the different methods outlined above.

4.2.4.5 Paired and multiple-site analyses

The Type B genetic, provenance and aggregate family-provenance correlation estimates for age 5 and age 8 are presented on tables 4.2.11 and 4.2.12 respectively. The latter estimates are presented for age 8 years for those pair-wise comparisons with the one 'additional' trial (PV34B1) where no 5-year assessments were available.

The proportions of the variance components for the provenance and family effects and their interactions at both 5 and 8-year volume, when analyzed across all tests in the series, are presented in table 4.2.13.

Table 4.2.9: Single-site within-provenance heritability (h^2_w) and aggregate family-provenance (h^2_a) heritability estimates for diameter at breast height (D5), total tree height (H5), height / diameter ratio (HD5) and volume per tree (V5) at 5 years of age in CAMCORE trial series 02 & 03.

Trait	Parameter	Test						Mean	Range
		20-10-02A	20-10-02B	20-07-02D	20-18-02E	20-10-03A1	20-10-03A2		
D5	h^2_w	0.10	0.42	0.23	0.35	0.17	0.26	0.25	0.10 – 0.42
	h^2_a	0.24	0.65	0.24	0.96	0.18	0.41	0.45	0.18 – 0.96
H5	h^2_w	0.11	0.39	0.27	0.25	0.22	0.36	0.26	0.11 – 0.39
	h^2_a	0.31	0.94	0.38	1.03	0.32	1.01	0.67	0.31 – 1.03
HD5	h^2_w	0.12	0.18	0.12	0.17	0.10	0.08	0.13	0.08 – 0.18
	h^2_a	0.15	0.19	0.15	0.26	0.12	0.10	0.16	0.10 – 0.26
V5	h^2_w	0.10	0.38	0.29	0.33	0.20	0.29	0.26	0.10 – 0.38
	h^2_a	0.30	0.74	0.35	1.10	0.25	0.61	0.56	0.25 – 1.10

Table 4.2.10: Single-site within-provenance (h^2_w) and aggregate family-provenance (h^2_a) heritability estimates for diameter at breast height (D8), total tree height (H8), height / diameter ratio (HD8) and volume per tree (V8) at 8 years of age in CAMCORE trial series 02 & 03.

Trait	Parameter	Test							Mean	Range
		20-10-02A	20-10-02B	20-18-02E	20-07-02D	20-10-03A1	20-10-03A2	34B1		
D8	h^2_w	0.10	0.44	0.31	0.21	0.17	0.30	0.20	0.25	0.10 – 0.44
	h^2_a	0.15	0.58	0.62	0.21	0.17	0.30	0.20	0.32	0.15 – 0.62
H8	h^2_w	0.11	0.39	0.30	0.16	0.21	0.59	0.24	0.29	0.11 – 0.59
	h^2_a	0.26	1.13	1.03	0.24	0.28	1.27	0.36	0.65	0.24 – 1.27
HD8	h^2_w	0.10	0.30	0.21	0.05	0.08	0.09	0.05	0.13	0.05 – 0.30
	h^2_a	0.17	0.68	0.21	0.08	0.16	0.55	0.19	0.29	0.08 – 0.68
V8	h^2_w	0.11	0.48	0.34	0.26	0.18	0.46	0.18	0.29	0.11 – 0.48
	h^2_a	0.22	0.83	0.84	0.26	0.19	0.47	0.19	0.43	0.19 – 0.84

Table 4.2.11: Type B genetic, provenance and aggregate family-provenance correlation estimates for all pairs of tests for diameter at breast height (D5), total tree height (H5), height / diameter ratio (HD5) and volume per tree (V5) at 5 years of age in CAMCORE trial series 02 & 03.

Paired sites		D5			H5			HD5			V5		
Test2	Test2	R _{Bg}	R _{bp}	R _{Bg} *	R _{Bg}	R _{bp}	R _{Bg} *	R _{Bg}	R _{bp}	R _{Bg} *	R _{Bg}	R _{bp}	R _{Bg} *
20-10-02A	20-10-02B	1.00	1.00	1.00	0.93	1.00	0.98	1.00	0.63	1.00	0.98	1.00	1.00
20-10-02A	20-18-02E	0.89	0.71	0.74	1.00	0.75	0.69	0.83	0.65	0.79	0.87	0.74	0.67
20-10-02A	20-07-02D	0.82	0.56	0.68	0.76	0.72	0.71	0.85	0.00	0.48	0.63	0.87	0.69
20-10-02B	20-07-02D	0.49	0.65	0.41	0.59	0.73	0.50	0.08	0.50	0.11	0.47	1.00	0.60
20-10-02B	20-18-02E	0.79	0.89	0.85	0.75	0.97	0.93	0.52	1.00	0.62	0.68	0.71	0.70
20-07-02D	20-18-02E	0.69	0.28	0.32	0.74	0.55	0.51	0.54	0.36	0.51	0.69	0.62	0.53
20-10-03A1	20-10-03A2	0.50	0.60	0.61	0.67	0.75	0.69	0.19	1.00	0.42	0.57	0.87	0.74
	Mean	0.74	0.67	0.66	0.78	0.78	0.71	0.57	0.59	0.56	0.70	0.83	0.70
	Minimum	0.49	0.28	0.32	0.59	0.55	0.50	0.08	0.00	0.11	0.47	0.62	0.53
	Maximum	1.00	1.00	1.00	1.00	1.00	0.98	1.00	1.00	1.00	0.98	1.00	1.00

*Aggregate family – provenance type B genetic correlation

Table 4.2.12: Type B genetic, provenance and aggregate family-provenance correlation estimates for all those comparisons between the CAMCORE trials and the 1 ‘additional’ test (PV34B1) for diameter at breast height (D8), total tree height (H8), height / diameter ratio (HD8) and volume per tree (V8) at 8 years of age in CAMCORE trial series 02 & 03.

Paired sites		D8			H8			HD8			V8		
Test1	Test2	R _{Bg}	R _{bp}	R _{Bg} *	R _{Bg}	R _{bp}	R _{Bg} *	R _{Bg}	R _{bp}	R _{Bg} *	R _{Bg}	R _{bp}	R _{Bg} *
20-10-02A	PV34B1	0.32	1.00	0.43	0.58	1.00	0.75	0.90	1.00	1.00	0.42	0.99	0.48
20-10-02B	PV34B1	0.17	1.00	0.23	0.29	0.82	0.53	0.57	1.00	0.73	0.19	1.00	0.24
20-07-02D	PV34B1	0.59	*	0.58	0.72	1.00	0.77	0.00	1.00	0.29	0.80	*	0.78
20-18-02E	PV34B1	0.50	0.00	0.01	0.59	0.39	0.33	1.00	0.96	1.00	0.60	0.13	0.32
	Mean	0.39	0.67	0.31	0.54	0.80	0.60	0.62	0.99	0.75	0.51	0.71	0.46
	Minimum	0.17	0.00	0.01	0.29	0.39	0.33	0.00	0.96	0.29	0.19	0.13	0.24
	Maximum	0.59	1.00	0.58	0.72	1.00	0.77	1.00	1.00	1.00	0.80	1.00	0.78

*Aggregate family – provenance type B genetic correlation

Table 4.2.13: The proportions of the variance components for the provenance, family with provenance and aggregate family/provenance family effects and their interactions at both 5 and 8 years for volume in CAMCORE trial series 02 & 03, analyzed across all tests.

Parameters estimated	Proportions	5-year data
Fam(Prov) / Fam(Prov) + Fam x Env.**	$\sigma_{f(p)}^2 / \sigma_{f(p)}^2 + \sigma_{fe}^2$	0.73
Prov / Prov + Prov x Env.*	$\sigma_p^2 / \sigma_p^2 + \sigma_{pe}^2$	0.80
agg. Fam / agg. Fam + agg.Fam x Env.***	$\sigma_f^2 / \sigma_f^2 + \sigma_{fe}^2$	0.70
Prov x Env. / Prov	$\sigma_{pe}^2 / \sigma_p^2$	0.25
Fam(Prov) x Env. / Fam(Prov)	$\sigma_{fe}^2 / \sigma_{f(p)}^2$	0.38
agg. Fam x Env. / agg. Fam	$\sigma_{fe}^2 / \sigma_f^2$	0.43

*Refers to the ratio of provenance variance over the combined provenance and provenance x environment variance – this is equivalent to a Type B provenance correlation from a paired site analysis.

**Refers to the family within provenance ratio of family variance over the combined family and family x environment variance – this is equivalent to a Type B genetic correlation from a paired site analysis.

***Refers to the aggregate family-provenance ratio of genetic variance over the combined genetic and genetic x environment variance – this is equivalent to a aggregate Type B genetic correlation from a paired site analysis.

4.2.4.6 Discussion

Within-provenance single-site heritability estimates calculated for all tests generally ranged between 0.10 and 0.40 for all traits at both 5 and 8 years of age (Table 4.2.9 & 4.2.10). A single-site heritability of at least 0.05 for both pairs of tests was considered to be a minimum requirement necessary to calculate Type B genetic correlations (Hodge and Dvorak, 1999). The estimates for volume were on average between 0.10 and 0.38 with little increase between the ages of 5 and 8 years. There did not appear to be any clear trends between single-site within-provenance heritability estimates amongst the other traits assessed. The only exception to the above was the height / diameter ratios where the heritabilities were, in most cases, much lower than for diameter, height or volume. This varied for this latter trait considerably however, with some tests exhibiting clear genetic differences with a maximum estimated within-provenance heritability of 0.30 at 8 years (Table 4.2.10). As expected, the single-site aggregate family-provenance heritability estimates calculated were generally much higher than the former within-provenance heritability estimates.

The Type B provenance correlations between pairs of tests for volume, were generally marginally higher (around 0.60 – 0.83) than for the family within provenance Type B genetic correlations at around 0.50 - 0.70 (Table 4.2.11 and 4.2.12). In other words, the provenance by site interaction is slightly lower than the family within provenance by site interaction. This is surprising in this series because it includes provenances from a broader geographic range – a central provenance to southern provenances. The central provenance of Potrero de Monroy was only represented by 3 families in most tests and that may have prejudiced these results. Despite this however, the two provenances of Santa Mario Papalo and Ixtlan occur in a more northern mountain range in

Oaxaca and would be expected to behave quite differently to the provenances of El Tlacuache and El Manzanal that occur in the more southern Sierra Madre del Sur range.

The overall average aggregate provenance-family Type B genetic correlations for volume, were around 0.46 at 8 years in test pairs with PV34B1, versus 0.70 for all the other test pairs at 5 years. Similar trends were apparent amongst the other growth traits assessed (Table 4.2.11 and 4.2.12). The average for the 8 year comparisons between all tests and the one additional test (PV34B1) are lower for possible similar reasons as discussed in section 4.2.3.6. Although the GxE for the height to diameter ratios (HD) differed from that of the other growth traits, no clear trends were apparent.

The overall ratio of GxE variance to genetic variance for volume at 5 years varies between 0.25 for provenance to 0.43 for the aggregate provenance-family estimates (Table 7.2.13). The estimates of the ratios of genetic to genetic plus GxE when analysed across all sites is comparable to the means of the paired site, Type B correlation estimates (see Table 4.2.11 & 4.2.13).

4.2.5 Analysis of the 05, 06 and 07 series of trials

4.2.5.1 Introduction

These trial series tested 8 sources of *P. patula* collected from locations in Mexico. These include the provenances of Potrero de Monroy, Conrado Castillo, Cuajimoloyas, Tlacotla, Pinal de Amoles, Zacualtipan, Llano de las Carmonas and Carrizal de Bravo. All of these provenances belong to the *P. patula* var. *patula* with the exception of the Cuajimoloyas and Carrizal de Bravo provenances, which are classified as being part of the *P. patula* var. *longipedunculata*.

4.2.5.2 Trial composition

The full details of the composition of each trial is presented in appendix 5. A matrix of the number of common treatments in each of a pair of trials is presented in table 4.2.14.

4.2.5.3 Trial design, management and site details

These 3 series contain 15 tests. The sites ranged from Mariti in the north, in Mpumalanga province, through KwaZulu-Natal (KZN), to Ugie in the South in the Eastern Cape province. This range spans much of the summer rainfall area of South Africa that has been planted up with

commercial, exotic plantations. Some further details of the exact location and basic climatic data are presented in appendix 1. The trial design for these CAMCORE tests has been described previously and was the same at all locations. All trees were planted at a spacing between tree of 3m x 3m in each test.

4.2.5.4 Single-site analyses

Single-site heritability estimates for growth characteristics at 5 & 8 years respectively are presented in tables 4.2.15 & 4.2.16, using the different methods outlined above.

4.2.5.5 Paired and multiple-site analyses

The Type B genetic, provenance and aggregate family-provenance correlation estimates for age 5 and age 8 are presented on tables 4.2.17 and 4.2.18 respectively. The latter estimates are presented for age 8 years for those pair wise comparisons with the two 'additional' trials (PV34B2 & PV34C2) where no 5-year assessments were available.

The proportions of the variance components for the provenance and family effects and their interactions at both 5 and 8-year volume, when analyzed across all tests in the series, are presented in table 4.2.19.

Table 4.2.14: Number of individual OP families common to each pair of trials in all 15 tests of the CAMCORE 05, 06 & 07 series.

	20-10-05F	20-10-05E1	20-10-05E2	20-07-05L	20-18-05K	20-10-06B1	20-10-06B2	20-07-06E	20-18-06D	20-10-07B1	20-10-07B2	20-07-07D	20-18-07A	PV34B2	PV34C2
20-10-05F	64	59	54	55	55	4	2	4	3	4	0	4	4	43	28
20-10-05E1	*	59	53	55	54	4	2	4	3	4	0	4	4	43	28
20-10-05E2	*	*	54	52	52	3	2	3	2	3	0	3	3	43	28
20-07-05L	*	*	*	55	52	3	2	3	3	3	0	3	3	43	28
20-18-05K	*	*	*	*	55	3	2	3	3	3	0	3	3	43	28
20-10-06B1	*	*	*	*	*	43	31	31	32	26	14	21	21	19	16
20-10-06B2	*	*	*	*	*	*	31	28	28	19	14	18	19	19	16
20-07-06E	*	*	*	*	*	*	*	31	27	20	14	19	20	19	16
20-18-06D	*	*	*	*	*	*	*	*	32	18	13	17	18	19	16
20-10-07B1	*	*	*	*	*	*	*	*	*	45	23	30	29	15	14
20-10-07B2	*	*	*	*	*	*	*	*	*	*	23	22	21	15	14
20-07-07D	*	*	*	*	*	*	*	*	*	*	*	30	27	15	14
20-18-07A	*	*	*	*	*	*	*	*	*	*	*	*	29	15	14
PV34B2	*	*	*	*	*	*	*	*	*	*	*	*	*	65	46
PV34C2	*	*	*	*	*	*	*	*	*	*	*	*	*	*	47

Shaded cells refer to pairs with less than 20 OP families in common.

Table 4.2.15: Single-site within-provenance (h^2_w) and aggregate family-provenance (h^2_a) heritability estimates for diameter at breast height (D5), total tree height (H5), height / diameter ratio (HD5) and volume per tree (V5) at 5 years of age in CAMCORE trial series 05, 06 & 07.

Trait	Parameter	Test													Mean	Range
		20-10-05F	20-10-05E1	20-10-05E2	20-07-05L	20-18-05K	20-10-06B1	20-10-06B2	20-07-06E	20-18-06D	20-10-07B1	20-10-07B2	20-07-07D	20-18-07A		
D5	h^2_w	0.22	0.25	0.13	0.30	0.20	0.08	0.12	0.20	0.16	0.07	0.15	0.10	0.12	0.16	0.07 – 0.30
	h^2_a	0.27	0.25	0.13	0.35	0.24	0.30	0.24	0.38	0.22	0.16	0.45	0.18	0.17	0.26	0.13 – 0.45
H5	h^2_w	0.21	0.20	0.05	0.18	0.16	0.13	0.09	0.38	0.25	0.14	0.12	0.26	0.13	0.18	0.05 – 0.38
	h^2_a	0.31	0.28	0.06	0.38	0.17	0.22	0.12	0.58	0.26	0.36	0.52	0.35	0.29	0.30	0.06 – 0.58
HD5	h^2_w	0.13	0.18	0.12	0.22	0.17	0.13	0.06	0.06	0.11	0.06	0.00	0.05	0.12	0.11	0.00 – 0.22
	h^2_a	0.18	0.19	0.14	0.23	0.20	0.29	0.20	0.33	0.20	0.14	0.08	0.16	0.17	0.19	0.08 – 0.33
V5	h^2_w	0.24	0.22	0.11	0.26	0.22	0.07	0.13	0.33	0.24	0.10	0.16	0.18	0.13	0.18	0.07 – 0.33
	h^2_a	0.31	0.27	0.11	0.39	0.26	0.23	0.23	0.51	0.30	0.25	0.36	0.27	0.26	0.29	0.11 – 0.51

Table 4.2.16: Single-site within-provenance (h^2_w) and aggregate family-provenance (h^2_a) heritability estimates for diameter at breast height (D8), total tree height (H8), height / diameter ratio (HD8) and volume per tree (V8) at 8 years of age in CAMCORE trial series 05, 06 & 07.

Trait	Parameter	Test														Mean	Range	
		20-10-05F	20-10-05E	20-10-05E	20-07-05L	20-18-05K	20-10-06B	20-10-06B	20-07-06E	20-18-06D	20-10-07B	20-10-07B	20-07-07D	20-18-07A	34 B2			34 C2
		1	2			1	2			1	2							
D8	h^2_w	0.23	0.24	0.21	0.22	0.17	0.11	0.14	0.14	0.15	0.09	0.16	0.13	0.11	0.17	0.19	0.17	0.09 – 0.24
	h^2_a	0.25	0.24	0.25	0.23	0.21	0.25	0.28	0.29	0.25	0.19	0.34	0.19	0.14	0.20	0.35	0.24	0.14 – 0.35
H8	h^2_w	0.22	0.21	0.10	0.12	0.13	0.22	0.23	0.22	0.36	0.14	0.22	0.07	0.11	0.02	0.18	0.17	0.02 – 0.36
	h^2_a	0.49	0.38	0.10	0.27	0.16	0.26	0.31	0.40	0.39	0.26	0.45	0.14	0.26	0.23	0.28	0.29	0.10 – 0.49
HD8	h^2_w	0.12	0.20	0.21	0.07	0.16	0.09	0.07	0.01	0.17	0.07	0.12	0.01	0.11	0.26	0.11	0.12	0.01 – 0.26
	H^2_a	0.21	0.29	0.26	0.09	0.20	0.23	0.23	0.20	0.40	0.24	0.32	0.10	0.22	0.29	0.21	0.23	0.09 – 0.40
V8	h^2_w	0.25	0.25	0.20	0.24	0.19	0.15	0.18	0.26	0.25	0.12	0.19	0.16	0.12	0.10	0.22	0.19	0.10 – 0.26
	H^2_a	0.34	0.30	0.23	0.29	0.25	0.25	0.32	0.40	0.31	0.23	0.36	0.21	0.20	0.20	0.41	0.29	0.20 – 0.41

Table 4.2.17: Type B genetic, provenance and aggregate family-provenance correlation estimates for all pairs of tests for diameter at breast height (D5), total tree height (H5), height / diameter ratio (HD5) and volume per tree (V5) at 5 years of age in CAMCORE trial series 05, 06 & 07.

Paired sites		D5			H5			HD5			V5		
Test1	Test2	R _{Bg}	R _{bp}	R _{Bg} *	R _{Bg}	R _{bp}	R _{Bg} *	R _{Bg}	R _{bp}	R _{Bg} *	R _{Bg}	R _{bp}	R _{Bg} *
20-10-05F	20-10-05E1	0.72	0.75	0.71	0.80	0.99	0.84	0.79	1.00	0.83	0.72	0.75	0.71
20-10-05F	20-10-05E2	0.56	0.71	0.56	0.53	0.00	0.24	0.77	1.00	0.82	0.36	0.00	0.26
20-10-05F	20-07-05L	0.87	0.97	0.89	0.89	1.00	0.96	0.88	0.82	0.88	0.89	1.00	0.93
20-10-05F	20-18-05K	0.75	0.48	0.73	0.75	0.14	0.63	0.80	0.77	0.80	0.77	0.31	0.73
20-10-05E1	20-10-05E2	0.78	0.00	0.79	0.65	0.30	0.57	0.76	1.00	0.78	0.63	0.40	0.59
20-10-05E1	20-07-05L	0.69	0.80	0.69	0.71	0.88	0.75	0.73	1.00	0.77	0.65	0.83	0.66
20-10-05E1	20-18-05K	0.66	0.00	0.57	0.68	0.35	0.60	0.58	0.81	0.59	0.74	0.00	0.64
20-10-05E2	20-07-05L	0.53	0.22	0.48	0.78	0.00	0.33	0.58	1.00	0.62	0.38	0.04	0.26
20-10-05E2	20-18-05K	0.77	0.00	0.70	0.92	0.00	0.80	0.79	1.00	0.83	0.62	0.00	0.52
20-07-05L	20-18-05K	0.70	0.92	0.73	0.78	0.45	0.65	0.75	0.98	0.76	0.73	0.58	0.71
20-10-06B1	20-10-06B2	0.58	0.85	0.73	0.61	0.00	0.53	0.19	0.94	0.65	0.77	0.88	0.82
20-10-06B1	20-07-06E	0.37	0.25	0.31	0.81	0.00	0.31	0.25	0.77	0.58	0.32	0.00	0.17
20-10-06B1	20-18-06D	0.82	0.40	0.65	0.95	0.00	0.81	0.70	0.50	0.58	0.71	0.32	0.63
20-10-06B1	20-10-07B1	1.00	0.95	1.00	1.00	0.92	1.00	0.76	1.00	0.92	1.00	0.81	1.00
20-10-06B1	20-07-07D	0.44	0.00	0.00	0.81	0.00	0.19	0.40	0.65	0.55	0.44	0.00	0.00
20-10-06B1	20-18-07A	0.38	0.00	0.00	0.78	0.00	0.63	0.46	0.64	0.54	0.54	0.00	0.07
20-10-06B2	20-07-06E	0.57	0.74	0.66	0.68	0.00	0.49	1.00	0.98	1.00	0.27	0.16	0.27
20-10-06B2	20-18-06D	0.75	1.00	0.88	0.56	0.00	0.45	0.42	0.66	0.50	0.55	1.00	0.65
20-07-06E	20-18-06D	0.48	0.98	0.67	0.77	0.06	0.52	0.19	0.91	0.65	0.51	0.57	0.51
20-07-06E	20-10-07B1	1.00	0.74	0.91	0.95	0.69	0.78	0.28	0.90	0.66	0.83	0.53	0.74
20-07-06E	20-18-07A	0.83	0.89	0.88	1.00	0.92	1.00	0.66	0.92	0.76	0.97	0.80	0.95
20-10-07B1	20-10-07B2	1.00	0.66	0.95	0.77	0.91	0.84	0.49	0.46	0.64	1.00	1.00	1.00
20-10-07B1	20-07-07D	0.29	0.22	0.30	1.00	0.40	0.70	0.50	0.80	0.71	0.48	0.26	0.39
20-10-07B1	20-18-07A	1.00	0.64	0.94	0.92	0.93	0.93	1.00	0.70	0.99	0.85	0.79	0.87
20-10-07B2	20-07-07D	0.85	0.00	0.25	0.45	0.02	0.24	0.01	0.37	0.63	0.60	0.00	0.22
20-10-07B2	20-18-07A	0.97	0.70	0.57	0.60	0.90	0.71	1.00	0.00	0.52	0.87	0.66	0.66
20-07-07D	20-18-07A	0.29	0.75	0.44	0.82	0.71	0.76	0.28	1.00	0.70	0.56	0.76	0.60
	Mean	0.69	0.54	0.63	0.78	0.39	0.64	0.59	0.80	0.71	0.66	0.46	0.58
	Minimum	0.29	0.00	0.00	0.45	0.00	0.19	0.01	0.00	0.50	0.27	0.00	0.00
	Maximum	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

*Aggregate family – provenance type B genetic correlation

Table 4.2.18: Type B genetic, provenance and aggregate family-provenance correlation estimates for all those comparisons between the CAMCORE trials and the 2 ‘additional’ tests (PV34B2 & PV34C2) for diameter at breast height (D8), total tree height (H8), height / diameter ratio (HD8) and volume per tree (V8) at 8 years of age in CAMCORE trial series 05, 06 & 07.

Paired Sites		D8			H8			HD8			V8		
Test1	Test2	r _{Bg}	r _{bp}	r _{bg} *	r _{Bg}	r _{bp}	R _{bg} *	r _{Bg}	r _{bp}	r _{bg} *	r _{Bg}	r _{bp}	r _{bg} *
20-10-05F	PV34B2	0.97	1.00	0.98	0.74	1.00	0.92	1.00	0.79	1.00	0.95	1.00	1.00
20-10-05F	PV34C2	0.91	0.00	0.70	0.78	0.85	0.82	1.00	0.58	0.86	0.90	0.30	0.65
20-10-05E1	PV34B2	0.69	1.00	0.75	0.46	0.95	0.72	0.84	1.00	0.88	0.62	0.94	0.73
20-10-05E1	PV34C2	0.93	0.05	0.78	0.80	0.83	0.81	1.00	1.00	1.00	0.81	0.09	0.52
20-10-05E2	PV34B2	0.60	0.73	0.63	0.45	0.24	0.44	0.75	1.00	0.81	0.38	0.09	0.39
20-10-05E2	PV34C2	0.87	0.60	0.77	0.93	1.00	0.92	1.00	1.00	1.00	0.60	0.23	0.41
20-07-05L	PV34B2	0.87	1.00	0.92	0.52	1.00	0.86	1.00	1.00	1.00	0.72	1.00	0.82
20-07-05L	PV34C2	1.00	0.48	0.97	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.70	1.00
20-18-05K	PV34B2	0.73	1.00	0.78	0.72	0.77	0.82	0.76	1.00	0.80	0.71	1.00	0.80
20-18-05K	PV34C2	0.53	1.00	0.74	0.35	1.00	0.53	1.00	1.00	1.00	0.46	0.93	0.65
PV34C2	PV34B2	0.85	1.00	0.89	0.58	0.77	0.73	0.80	1.00	0.85	0.74	0.84	0.78
	Mean	0.81	0.69	0.81	0.67	0.86	0.78	0.92	0.94	0.93	0.72	0.65	0.70
	Minimum	0.53	0.00	0.63	0.35	0.24	0.44	0.75	0.58	0.80	0.38	0.09	0.39
	Maximum	1.00	1.00	0.98	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

*Aggregate family – provenance type B genetic correlation

Table 4.2.19: The proportions of the variance components for the provenance, family with provenance and aggregate family-provenance family effects and their interactions at both 5 and 8 years for volume in CAMCORE trial series 05, 06 & 07, analyzed across all tests separately for each series.

Parameters estimated	Proportions	5-year data
Series 05		
Fam(Prov) / Fam(Prov) + Fam x Env.**	$\sigma_{f(p)}^2 / \sigma_{f(p)}^2 + \sigma_{fe}^2$	0.69
Prov / Prov + Prov x Env.*	$\sigma_p^2 / \sigma_p^2 + \sigma_{pe}^2$	0.48
agg. Fam / agg. Fam + agg.Fam x Env.***	$\sigma_f^2 / \sigma_f^2 + \sigma_{fe}^2$	0.63
Fam(Prov) x Env. / Fam(Prov)	$\sigma_{fe}^2 / \sigma_{f(p)}^2$	0.45
Prov x Env. / Prov	$\sigma_{pe}^2 / \sigma_p^2$	1.10
agg. Fam x Env. / agg. Fam	$\sigma_{fe}^2 / \sigma_f^2$	0.60
Series 06		
Fam(Prov) / Fam(Prov) + Fam x Env.**	$\sigma_{f(p)}^2 / \sigma_{f(p)}^2 + \sigma_{fe}^2$	0.43
Prov / Prov + Prov x Env.*	$\sigma_p^2 / \sigma_p^2 + \sigma_{pe}^2$	0.33
agg. Fam / agg. Fam + agg.Fam x Env.***	$\sigma_f^2 / \sigma_f^2 + \sigma_{fe}^2$	0.40
Fam(Prov) x Env. / Fam(Prov)	$\sigma_{fe}^2 / \sigma_{f(p)}^2$	1.31
Prov x Env. / Prov	$\sigma_{pe}^2 / \sigma_p^2$	2.06
agg. Fam x Env. / agg. Fam	$\sigma_{fe}^2 / \sigma_f^2$	1.48
Series 07		
Fam(Prov) / Fam(Prov) + Fam x Env.**	$\sigma_{f(p)}^2 / \sigma_{f(p)}^2 + \sigma_{fe}^2$	0.60
Prov / Prov + Prov x Env.*	$\sigma_p^2 / \sigma_p^2 + \sigma_{pe}^2$	0.69
agg. Fam / agg. Fam + agg.Fam x Env.***	$\sigma_f^2 / \sigma_f^2 + \sigma_{fe}^2$	0.63
Fam(Prov) x Env. / Fam(Prov)	$\sigma_{fe}^2 / \sigma_{f(p)}^2$	0.68
Prov x Env. / Prov	$\sigma_{pe}^2 / \sigma_p^2$	0.45
agg. Fam x Env. / agg. Fam	$\sigma_{fe}^2 / \sigma_f^2$	0.60

*Refers to the ratio of provenance variance over the combined provenance and provenance x environment variance – this is equivalent to a Type B provenance correlation from a paired site analysis.

**Refers to the family within provenance ratio of family variance over the combined family and family x environment variance – this is equivalent to a Type B genetic correlation from a paired site analysis.

***Refers to the aggregate family-provenance ratio of genetic variance over the combined genetic and genetic x environment variance – this is equivalent to an aggregate Type B genetic correlation from a paired site analysis.

4.2.5.6 Discussion

Single-site within-provenance heritability estimates calculated for all tests generally ranged between 0.07 and 0.36 for all traits at both 5 and 8 years of age (Table 4.2.15 & 4.2.16). A single-site within-provenance heritability estimate of at least 0.05 for both pairs of tests was considered to be a minimum requirement necessary to calculate Type B genetic correlations (Hodge and Dvorak, 1999). The estimates for volume were on average around 0.18 with little increase between the ages of 5 and 8 years. There did not appear to be any clear trends between single-site heritability within-provenance estimates amongst the other traits assessed. The only exception to the above was the height / diameter ratios where the heritabilities were in most cases much lower than for diameter, height or volume. This varied for the latter trait

considerably, however, with some tests exhibiting clear genetic differences with a maximum estimated family within provenance heritability estimate of 0.30 at 8 years (Table 4.2.16). As expected the single-site aggregate family-provenance heritability estimates calculated were generally much higher than the former within-provenance heritabilities.

The Type B provenance correlations between pairs of tests for volume, were generally lower (around 0.46 – 0.65) than for the family within provenance Type B genetic correlations at around 0.58 - 0.70 (Table 4.2.17 and 4.2.18). In other words the provenance by site interaction is slightly higher than the family within provenance by site interaction. This is in contrast to the situation in the series 1 - 4 where the opposite effect was found. It would be expected that the provenances tested would have a strong influence on the amount of GxE and thus this finding is not entirely surprising. In this case a wide geographic range of provenances was sampled from that at Conrado Castillo in the north to Cuajimoloyas in the south of Mexico.

The overall average aggregate provenance-family Type B genetic correlations for volume, were around 0.70 at 8 years in tests paired with PV34B2 / C2 and 0.46 for all the other test pairs at 5 years. Similar trends were apparent amongst the other growth traits assessed (Table 4.2.17 & 4.2.18). In contrast to the series 1 – 4 tests the average for the 8-year comparisons between all tests and the two additional tests (PV34B2 & C21) are higher. Although the GxE for the height to diameter ratios (HD) differed from that of the other growth traits, no clear trends were apparent.

The overall ratio of GxE variance to genetic variance for volume at 5 years varies between 0.45 for provenance to 0.60 for the aggregate provenance-family estimates for series 05 and 07 (Table 7.2.19). Series 06 has a particularly high level of GxE with the provenance at around 2.00 and aggregate provenance family at 1.50. The estimates of the ratios of genetic to genetic plus GxE when analysed across all sites is comparable to the means of the paired site, Type B correlation estimates (see Table 4.2.17 & 4.2.19), particularly when considering the individual series. The discrepancy is much smaller than in the s0104 series. This is particularly true if comparing only the Type B genetic correlations for a particular series. In this particular case, one can make an accurate comparison in that each series was analyzed separately. For example, the average for the 6 aggregate family-provenance Type B genetic correlation estimates for series 07 is 0.62 and the overall ratio for that series is 0.63 (Table 4.2.17 & 4.2.19).

4.2.6 Analysis of the 08 and 09 series of trials

4.2.6.1 Introduction

These trial series tested 6 sources of *P. patula* collected from locations in Mexico. These include the provenances of Potrero de Monroy, El Cielo, La Encarnacion, La Cruz, Cumbre de Muridores and Cruz Blanca. All of these provenances belong to the *P. patula* var. *patula*.

4.2.6.2 Trial composition

Details of the composition of each trial are presented in appendix 6. A matrix of the number of common treatments in each of a pair of trials is presented in table 4.2.20.

4.2.6.3 Trial design, management and site details

These 2 series contain 5 tests. The sites are all confined to the Mpumalanga province and range from Tweefontein in the north to Jessievale in the South. This range is relatively restricted but does include a range of site types from warm, wet sites to relatively cold, dry sites. Some details of the exact location and basic climatic data are presented in appendix, and for 20-07-08C in table 4.2.1. The trial design for these CAMCORE tests has been described previously and was the same at all locations. All trees were planted at a spacing of 3m x 3m in each test. The Helvetia A39 trial (200708C) was measured at 7 years as opposed to 5 years for the other 4 tests.

4.2.6.4 Single-site analyses

Single-site heritability estimates for growth characteristics at 5 years are presented in table 4.2.21, using the different methods outlined above.

4.2.6.5 Paired and multiple-site analyses

The Type B genetic, provenance and aggregate family-provenance correlation estimates are presented on tables 4.2.22.

The proportions of the variance components for the provenance and family effects and their interactions at both 5 and 8-year volume, when analyzed across all tests in the series, are presented in table 4.2.23.

Table 4.2.20: Number of individual OP families common to each pair of trials in all 5 tests of the CAMCORE 08 & 09 series.

	20-10-08A	20-07-08C	20-18-08B	20-07-09B	20-18-09A
20-10-08A	54	54	54	6	6
20-07-08C	*	54	54	6	6
20-18-08B	*	*	54	6	6
20-07-09B	*	*	*	50	45
20-18-09A	*	*	*	*	51

Shaded cells refer to pairs with less than 20 OP families in common.

Table 4.2.21: Single-site family within-provenance (h^2_w) and aggregate family-provenance (h^2_a) heritability estimates for diameter at breast height (D5), total tree height (H5), height / diameter ratio (HD5) and volume per tree (V5) at 5 years* of age in CAMCORE trial series 08 & 09.

		Test					Mean	Range
Trait	Parameter	20-10-08A	20-07-08C	20-18-08B	20-07-09B	20-18-09A		
D5	h^2_w	0.13	0.08	0.05	0.19	0.11	0.11	0.05 – 0.19
	h^2_a	0.19	0.11	0.11	0.20	0.14	0.15	0.11 – 0.20
H5	h^2_w	0.12	0.10	0.07	0.21	0.17	0.13	0.07 – 0.21
	h^2_a	0.26	0.14	0.19	0.26	0.22	0.21	0.14 – 0.26
HD5	h^2_w	0.18	0.07	0.19	0.09	0.15	0.14	0.07 – 0.19
	h^2_a	0.20	0.10	0.23	0.09	0.17	0.16	0.09 – 0.23
V5	h^2_w	0.10	0.08	0.05	0.23	0.15	0.12	0.05 – 0.23
	h^2_a	0.21	0.11	0.12	0.24	0.19	0.17	0.11 – 0.24

*20-07-08C was assessed at 7 years.

Table 4.2.22: Type B genetic, provenance and aggregate family-provenance correlation estimates for all pairs of tests for diameter at breast height (D5), total tree height (H5), height / diameter ratio (HD5) and volume per tree (V5) at 5 years of age in CAMCORE trial series 08 & 09.

Paired sites		D5			H5			HD5			V5		
Test1	Test2	R_{Bg}	R_{bp}	R_{Bg}^*	R_{Bg}	R_{bp}	R_{Bg}^*	R_{Bg}	R_{bp}	R_{Bg}^*	R_{Bg}	R_{bp}	R_{Bg}^*
20-10-08A	20-07-08C	0.82	0.00	0.36	0.66	0.21	0.44	0.78	0.84	0.78	0.82	0.00	0.24
20-10-08A	20-18-08B	0.54	0.03	0.37	0.41	0.65	0.51	0.84	0.90	0.85	0.46	0.17	0.30
20-10-08A	20-07-09B	*	0.42	*	*	0.86	*	*	1.00	*	*	0.44	*
20-10-08A	20-18-09A	*	0.00	*	*	0.00	*	*	0.45	*	*	0.00	*
20-07-08C	20-18-08B	1.00	0.77	1.00	0.80	1.00	0.92	0.78	1.00	0.83	1.00	0.79	0.93
20-07-08C	20-07-09B	*	0.00	*	*	0.00	*	*	1.00	*	*	0.00	*
20-07-08C	20-18-09A	*	1.00	*	*	0.00	*	*	1.00	*	*	0.72	*
20-18-08B	20-07-09B	*	0.00	*	*	0.00	*	*	1.00	*	*	0.00	*
20-18-08B	20-18-09A	*	0.53	*	*	0.00	*	*	1.00	*	*	0.00	*
20-07-09B	20-18-09A	0.78	0.00	0.69	0.60	0.00	0.46	0.73	1.00	0.75	0.75	0.00	0.64
	Mean	0.79	0.28	0.60	0.62	0.27	0.58	0.78	0.92	0.81	0.76	0.21	0.53
	Minimum	0.54	0.00	0.36	0.41	0.00	0.44	0.73	0.45	0.75	0.46	0.00	0.24
	Maximum	1.00	1.00	1.00	0.80	1.00	0.92	0.84	1.00	0.85	1.00	0.79	0.93

*Aggregate family – provenance type B genetic correlation

Table 4.2.23: The proportions of the variance components for the provenance, family with provenance and aggregate family/provenance family effects and their interactions at 5-years for volume in CAMCORE trial series 08 & 09, analyzed across all tests.

Parameters estimated	Proportions	5-year data
Prov / Prov + Prov x Env.*	$\sigma_p^2 / \sigma_p^2 + \sigma_{pe}^2$	0.00
Fam(Prov) / Fam(Prov) + Fam x Env.**	$\sigma_{f(p)}^2 / \sigma_{f(p)}^2 + \sigma_{fe}^2$	0.56
Agg. Fam / agg. Fam + agg.Fam x Env.***	$\sigma_f^2 / \sigma_f^2 + \sigma_{fe}^2$	0.35
Prov x Env. / Prov	$\sigma_{pe}^2 / \sigma_p^2$	*
Fam(Prov) x Env. / Fam(Prov)	$\sigma_{fe}^2 / \sigma_{f(p)}^2$	0.80
Agg. Fam x Env. / agg. Fam	$\sigma_{fe}^2 / \sigma_f^2$	1.90

*Refers to the ratio of provenance variance over the combined provenance and provenance x environment variance – this is equivalent to a Type B provenance correlation from a paired site analysis.

**Refers to the family within provenance ratio of family variance over the combined family and family x environment variance – this is equivalent to a Type B genetic correlation from a paired site analysis.

***Refers to the aggregate family-provenance ratio of genetic variance over the combined genetic and genetic x environment variance – this is equivalent to a aggregate Type B genetic correlation from a paired site analysis.

4.2.6.6 Discussion

Single-site within-provenance heritability estimates calculated for all tests generally ranged between 0.05 and 0.24 for all traits at 5 years of age (Table 4.2.21). A within-provenance heritability estimate of at least 0.05 for both pairs of tests was considered to be a minimum requirement necessary to calculate Type B genetic correlations (Hodge and Dvorak, 1999). The estimates for volume were on average 0.12. There did not appear to be any clear trends between single-site within-provenance heritability estimates between and amongst the other traits assessed. As expected the single-site aggregate family-provenance heritabilities calculated were generally much higher than the former within-provenance heritability estimates.

The Type B provenance correlations between pairs of tests was considerably lower (around 0.25) than for the family within provenance Type B genetic correlations which averaged around 0.75, see Table 4.2.22. In other words the provenance by site interaction is considerably larger than the family within provenance by site interaction.

The overall average aggregate provenance-family Type B genetic correlations were around 0.53 for volume with similar trends amongst the other growth traits assessed (Table 4.2.22). The height to diameter ratios (HD) differed somewhat from this overall trend. The level of GxE at the provenance level was actually less for this trait.

The overall ratio of GxE variance to genetic variance for volume at 5 years was high at 1.90 for the aggregate provenance-family estimates (Table 4.2.23). The provenance ratio was not able to be estimated because there was no significant provenance effect. The estimates of the ratios of

genetic to genetic plus GxE when analyzed across all sites is not comparable to the means of the paired site, Type B correlation estimates (see Table 4.2.22 & 4.2.23). The reason here is the same as for series 1-4, because not all the pairs were considered in the estimates of the Type B genetic correlations. The reason was that several pairs had too few families in common.

4.2.7 Analysis of the 10 series of trials

4.2.7.1 Introduction

This trial series tested 4 sources of *P. patula* collected from locations in Mexico. These include the provenances of Potrero de Monroy, Cruz Blanca and Calchahualco. All of these provenances belong to the *P. patula* var. *patula*.

4.2.7.2 Trial composition

Details of the composition of each trial is presented in appendix 7. A matrix of the number of common treatments in each of a pair of trials is presented in table 4.2.24.

Table 4.2.24: Number of individual OP families common to each pair of trials in all 3 tests of the CAMCORE 10 series.

	20-10-10C	20-07-10B	20-18-10E
20-10-10C	*	44	44
20-07-10B	*	*	50
20-18-10E	*	*	*

4.2.7.3 Trial design, management and site details

This series contain 3 tests, with 2 of the sites in the Mpumalanga province and 1 in KwaZulu-Natal (KZN). They range from Tweefontein in the north to Tetworth in KZN. Some further details of the exact location and basic climatic data are presented in appendix 1, and for 20-18-10E in table 4.2.1. The trial design for these CAMCORE tests has been described previously and was the same at all locations. All trees were planted at a spacing of 3m x 3m in each test.

4.2.7.4 Single-site analyses

Single-site heritability estimates for growth characteristics at 5 years are presented in table 4.2.25, using the different methods outlined above.

Table 4.2.25: Single-site within-provenance (h^2_w) and aggregate family-provenance (h^2_a) heritability estimates for diameter at breast height (D5), total tree height (H5), height / diameter ratio (HD5) and volume per tree (V5) at 5 years of age in CAMCORE trial series 10.

Trait	Test					
	Parameter	20-10-10C	20-07-10B	20-18-10E	Mean	Range
D5	h^2_w	0.04	0.11	0.01	0.05	0.01 – 0.11
	h^2_a	0.04	0.11	0.01	0.05	0.01 – 0.11
H5	h^2_w	0.03	0.18	0.08	0.10	0.03 – 0.18
	h^2_a	0.07	0.18	0.10	0.12	0.07 – 0.18
HD5	h^2_w	0.05	0.01	0.00	0.02	0.00 – 0.05
	H^2_a	0.05	0.01	0.00	0.02	0.00 – 0.05
V5	h^2_w	0.01	0.15	0.05	0.07	0.01 – 0.15
	H^2_a	0.03	0.15	0.05	0.08	0.03 – 0.15

4.2.7.5 Discussion

Single-site within-provenance heritability estimates for volume at 5 years, calculated for all 3 tests, varied between 0.01 and 0.15 at 5 years of age (Table 4.2.25). A single-site heritability of at least 0.05 for both pairs of tests was considered to be a minimum requirement necessary to calculate Type B genetic correlations (Hodge and Dvorak, 1999). It was thus not possible to estimate any Type B genetic correlations from these 3 tests because 2 of them had single-site heritabilities less than this.

4.2.8 Analysis of the 15 series of trials

4.2.8.1 Introduction

This trial series tested 2 sources of *P. patula* collected from locations in Mexico. These include the provenances of Sierra Huayacocotla and Acaxochitlan. Both of these two provenances belong to the *P. patula* var. *patula*.

4.2.8.2 Trial composition

Details of the composition of each trial is presented in appendix 8. A matrix of the number of common treatments in each of a pair of trials is presented in table 4.2.26.

Table 4.2.26: Number of individual OP families common to each pair of trials in all 3 tests of the CAMCORE 15 series.

	20-07-15E	20-10-15L	203*
20-07-15E	47	28	23
20-10-15L	*	46	14
R 203*	*	*	25

*R203 is an additional Sappi trial with some common families

4.2.8.3 Trial design, management and site details

This series contain 3 tests, with 2 of the sites in the Mpumalanga province and 1 in Swaziland. They range from Tweefontein in the north to Hlelo in the south, both in Mpumalanga province and further to the east at Usutu in Swaziland. Some further details of the exact location and basic climatic data are presented in appendix 1 and table 4.2.1. The trial design for these CAMCORE tests has been described previously and was the same at all locations. The exception is the trial (R203) at Usutu which was planted at a spacing between trees of 2.7 x 2.1 and consisted of only 5 tree line plots. All treatments were randomized with no provenance sub-blocking.

4.2.8.4 Single-site analyses

Single-site heritability estimates for growth characteristics at 3 years are presented in table 4.2.27, using the different methods outlined above.

Table 4.2.27: Single-site within-provenance (h^2_w) and aggregate family-provenance (h^2_a) heritability estimates for diameter at breast height (D3), total tree height (H3), height / diameter ratio (HD3) and volume per tree (V3) at 3 years of age in CAMCORE trial series 15.

Trait	Parameter	Test			Mean	Range
		20-10-15L	20-07-15E	R 203		
D3	h^2_w	0.00	0.26	0.34	0.20	0.00 – 0.34
	h^2_a	0.00	0.31	0.34	0.22	0.00 – 0.34
H3	h^2_w	0.03	0.22	0.16	0.14	0.03 – 0.22
	h^2_a	0.03	0.32	0.16	0.17	0.03 – 0.32
HD3	h^2_w	0.01	0.19	0.40	0.20	0.01 – 0.40
	H^2_a	0.02	0.19	0.40	0.21	0.02 – 0.40
V3	h^2_w	0.00	0.28	0.16	0.15	0.00 – 0.28
	H^2_a	0.00	0.35	0.16	0.17	0.00 – 0.35

4.2.8.5 Paired-site analyses

The Type B genetic, provenance and aggregate family-provenance correlation estimates are presented on table 4.2.28. Only two tests are available for analysis in this series so no multiple site analysis was carried out.

Table 4.2.28: Type B genetic correlation estimates for a single pair* of tests for diameter at breast height (D3), total tree height (H3), height / diameter ratio (HD3) and volume per tree (V3) at 3 years of age in CAMCORE trial series 15.**

Paired sites		D3	H3	HD3	V3	VI3
Test1	Test2	r_{Bg}	r_{Bg}	r_{Bg}	r_{Bg}	r_{Bg}
20-07-15E	R 203	0.73	0.74	0.64	0.63	0.65

*Only one pair met the criteria of $h^2w > 0.5$ & 20 common families.

**Only one provenance was represented in R203 and thus no r_{Bp} 's could be calculated.

4.2.8.6 Discussion

Single-site heritability estimates for volume ranged between 0 and 0.28 at 3 years of age (Table 4.2.27). A single-site within-provenance heritability estimate of at least 0.05 for both pairs of tests was considered to be a minimum requirement necessary to calculate Type B genetic correlations (Hodge and Dvorak, 1999). In this case only 2 tests were thus considered for paired site analysis. As expected the single-site aggregate family-provenance heritabilities calculated were generally much higher than the former within-provenance heritability estimate.

The within-provenance Type B genetic correlation was 0.63 for volume at 3 years of age (Table 4.2.28). The aggregate family-provenance Type B genetic correlation estimate for height to diameter ratios (HD) were also of similar magnitude.

4.3 Analysis of all FAO provenance trials in Southern Africa

4.3.1 Introduction and Methods

4.3.1.1 The entries in this particular trial series consisted of 12 bulked seedlots kept separate by provenance, acquired from collections made in Mexico by the Food and Health Organization of the United Nations (FAO) and supplied to South African Forestry organizations through the Oxford Forestry Institute. This material was planted on 8 sites in Southern Africa by 3 organizations Mondi Forests, Sappi Forests and the South African Forestry Research Institute (SAFRI).

4.3.1.2 Description of genotypes and test site details

The provenances represented in this trial series are presented in table 4.3.1. The genotypes represent bulk provenance collections made over a range of climatic areas in which *P. patula* is found in Mexico. In addition to the 12 Mexican provenances most of the tests also include at least one treatment originating from South Africa. These additional seedlots represent a measure of the South African land race and generally include an unimproved genetic check, as well as in some cases 1st and 2nd generation seed orchard material.

The trial series was planted across 8 sites in Southern Africa. Details of these 8 sites are provided in table 4.3.2 and represent a range of site types commonly planted to this species in the summer rainfall areas of Southern Africa.

All tests consisted of 4 replications and were planted during the summer season of 1990 / 1991. Further details of the nature of the trial design, plot size and assessment age for all 8 tests is outlined table 4.3.3.

4.3.1.3 Trial assessment and data preparation

The trials were assessed for diameter at breast height and overall tree height at 8 years of age. The one notable exception is the Maxwell trial which was measured at 10 years of age. Tree volumes were calculated in two ways using the same methodology, already described previously (see 4.2.2.1).

Table 4.3.1: Summary of the locations of *P. patula* provenances collected through the FAO in Mexico and supplied to South African Forestry organizations

Provenance	Equivalent Provenances	CAMCORE State	Lat.	Long.	Altitude (m)
Huachinago (Km158)	No equivalent provenance	Puebla	20°10' N	98°10' W	2030
Zacualtipan1*	Zacualtipan	Hidalgo	20°40' N	98°40' W	2000
Zacualtipan2*	Zacualtipan	Hidalgo	20°40' N	98°40' W	2000
Pinal de Amoles	Pinal de Amoles	Queretaro	20°40' N	99°42' W	2350
La Venta	No equivalent provenance	Hidalgo	20°08' N	99°30' W	2300
La Joya1*	Cruz Blanca	Veracruz	19°20' N	97°08' W	2100
La Joya2*	Cruz Blanca	Veracruz	19°36' N	97°08' W	2250
La Joya3*	Cruz Blanca	Veracruz	19°36' N	97°08' W	2160
Altotonga	No equivalent provenance	Veracruz	19°45' N	97°15' W	2210
Acaxotithan (Km5)	Acaxochitlan	Hidalgo	20°09' N	98°10' W	2030
Tlaoxtiipa	No equivalent provenance	Puebla	20°03' N	98°04' W	2000
Apizaco	Tlacotala	Tlaxcala	19°41' N	98°08' W	2760
Unimproved seedlot**		South Africa			
1 st generation seedlot**		South Africa			
2 nd generation seedlot**		South Africa			

*Represent different seedlots collected from the same geographical location (provenance)

**South African commercial seedlots entered in some of the tests

Table 4.3.2: Location and site details for all 8 tests in the FAO provenance series.

Test code	Company	Region	Location	Lat.	Long.	Alt.	Age*
822	Safcol	Mpumalanga	Wilgeboom B13b	24.980S	30.959E	960	8
821	Safcol	Mpumalanga	Tweefontein K29	24.986S	30.819E	1300	8
736	Safcol	Mpumalanga	Witklip H18	25.202S	30.938E	1110	8
PV34B2	Mondi	Mpumalanga	Magsleigh	25.221S	30.794E	1280	8
711	Safcol	Mpumalanga	Jessievale A6	26.232S	30.517E	1750	8
R 147	Sappi	Swaziland	Usutu D16	26.598S	30.928E	1524	8
PV34C2	Mondi	KZN	Goodhope	29.683S	29.980E	1340	8
PV039T	Sappi	KZN	Maxwell 12	30.035S	29.924E	1405	10

*Age assessed.

Table 4.3.3: Further details of the plot size, assessments and other comments for all 8 tests in the FAO provenance series.

Test code	Location	Plot size	Measured trees
822	Wilgeboom B13b	5x5 = 25 tree square plot	inner 3x3
821	Tweefontein K29	5x5 = 25 tree square plot	inner 3x3
736	Witklip H18	5x5 = 25 tree square plot	inner 3x3
PV34B2	Magsleigh	1x6 = 6 tree row plot	all
711	Jessievale A6	5x5 = 25 tree square plot	inner 3x3
R 147*	Usutu D16	5x5 = 25 tree square plot	all
PV34C2	Goodhope	4x6 = 24 tree square plot	all
PV039T	Maxwell 12	5x5 = 25 tree square plot	all

*Height was measured in a sample of 5 trees per plot only with Trees selected based on those with largest stem diameters at 5 years of age.

4.3.2 Single, paired and multiple-site analyses

4.3.2.1 Single-site analysis

For each test, a parameter P^2_b was estimated for all growth traits assessed, and for all tests separately. All South African seedlots were removed before this analysis. This parameter provides a measure of the relative proportion of the genetic component (due to provenance only in this case) compared to the overall level of variation. P^2_p was calculated as follows:-

$$P^2_b = \frac{\sigma^2_p}{\sigma^2_T}$$

where $\sigma^2_T = \sigma^2_p + \sigma^2_{p*b} + \sigma^2_e$

Variance components for all traits were estimated using the PROC MIXED procedure in SAS.

4.3.2.2 Paired-site analysis

Paired-site analyses were conducted for pairs of tests as outlined in chapter 3. In these analyses all genetic checks were removed and the data was standardized. Only Type B provenance

correlations could be obtained. A P^2_b of 0.02 was taken as a minimum level of precision to compare between 2 tests. These analyses were conducted in order to quantify the level of GxE among provenances amongst pairs of sites. The Type B provenance estimates are presented in table 4.3.5.

Table 4.3.4: Parameter estimate P^2_b for diameter at breast height (D8), total tree height (H8) and volume per tree (V8) at 8 / 10 years of age in the FAO trial series.

Trait	Parameter	Test							Mean	Range
		822	821	736	PV34B2	711	PV34C2	PV039		
D8	P^2_p	0.010	0.010	0.007	0.048	0.032	0.004	0.000	0.016	0.000 – 0.048
H8	P^2_p	0.102	0.000	0.028	0.036	0.000	0.042	0.000	0.030	0.000 – 0.102
V8	P^2_p	0.030	0.002	0.018	0.056	0.017	0.021	0.002	0.021	0.002 – 0.056

Table 4.3.5: Type B provenance correlation estimates for all pairs of tests for diameter at breast height (D8), total tree height (H8) and volume per tree (V8) at 8 years of age in the FAO trial series.

Paired sites		D8	H8	V8
Test1	Test2	r_{Bp}	r_{Bp}	r_{Bp}
821	736	*	1.00	*
821	PV34B2	*	1.00	1.00
821	711	*	*	*
821	PV34C2	*	1.00	0.00
736	PV34B2	*	1.00	*
736	PV34C2	*	0.55	*
PV34B2	711	0.00	*	*
PV34B2	PV34C2	*	0.97	0.00

4.3.3 Discussion

The variation due to provenance for these 8 tests was generally very low. The percentage of variation explained by provenance compared to total variance varied from 2 to 5.6% (Table 4.3.4). The result was that the overall estimates of the provenance by environment interaction was not precise. Type B provenance correlation estimates were only calculated for situations where both tests had P^2_b greater than 0.02. The result was that few Type B provenance correlations were estimated (Table 4.3.5) and those that were do not appear to contribute much useful information.

4.4 Analysis of a ICFR progeny trial series in Southern Africa

4.4.1 Introduction and Methods

4.4.1.1 The Institute for Commercial Forestry Research (ICFR) initiated a tree improvement program in 1990 that focused on *P. patula* in the KwaZulu-Natal (KZN) region of South Africa (Hagedorn, 1991). At that stage improved seed of the species was in short supply. The two oldest tree improvement programs (i.e. the state and Mondi) and their seed orchards were situated in the Mpumalanga region. All the selections for the latter two breeding programs originated from plantations in Mpumalanga and the Northern Provinces. In addition, it was suspected that GxE between this northern region and KZN may be substantial, and a breeding program utilizing selections from plantations in the KZN region, would be beneficial to the entire forest industry. Consequently, during 1994, a series of progeny trials with a set of open-pollinated (OP) families from the KZN selections was planted across a broad range of sites to look in more detail at the question of GxE (Hagedorn, 1995).

4.4.1.2 Description of genotypes and test site details

All five trials were represented by 48 identical treatments comprising 45 open-pollinated (OP) families and three genetic checks. One additional treatment included in the tests was not common to all sites and was either composed of a further OP family or an unimproved genetic check (Table 4.4.1). During 1990 the Institute for Commercial Forestry Research (ICFR), with the support of the South African forest industry, made a decision to embark on a comprehensive breeding programme with *P. patula* within the KwaZulu-Natal region. Plantations within this region were searched for plus trees and 533 selections were made (Hagedorn, 1993). Seed from these trees was collected and 12 sub-populations, planted out in breeding seedling orchards, were established within the region. The seed for the OP families entered within this trial series originate from this population. Families from a wide spectrum of the sub-populations were chosen, based entirely on the amount of additional seed available. At that stage no prior knowledge of the performance of these families was known.

Six trials were established over a period of two months in 1994. These sites ranged from Graskop in the north, in Mpumalanga province, through Swaziland and KZN, to Ugie in the south, in the North-Eastern.Cape Province. Further details of the exact position, planting and assessment times of the five trials reported in this paper, are provided in table 4.4.2. A sixth test planted at Pinewoods plantation, in the province of KZN experienced high mortality at planting and was not assessed further. The trials all received a low pruning to around 1.5m at 5 years and no thinning had been carried out up to the age of assessment at 6 years.

All six trials were planted as balanced 7x7 lattice designs with 8 replications and 49 treatments per trial. The plot size was a 4-tree line plot and all trees were planted at a spacing between trees of 3 x 3 m between trees. Two rows of trees, with similar composition as the trial, were planted around each trial as surrounds. All seedlings were raised at the ICFR nursery in Pietermaritzburg, KZN and were planted out over a period of two months during the early summer of 1994 (Table 4.4.3).

4.4.1.3 Trial assessment and data preparation

All five trials were assessed for height and DBH (diameter at breast height, i.e. 1.3m, in cm) during the spring and early summer of 2000. Although no formal crown or stem form assessments were made, any defects or abnormalities such as broken tops, forking or foxtailing was noted. The height and dbh measurements were used to calculate volume per tree, in m³ / tree, overbark, using the two methods outlined previously (see 4.2.2.1).

Table 4.4.1: Trial composition of the 5 progeny tests in the ICFR series.

Treatments	Graskop	Helvetia	Usutu	Bulwer	Ugie
45 OP families selected in plantations within the KZN region during 1990/91.	√	√	√	√	√
Family 279 - OP family selected in plantations within the KZN region during 1990/91.	√	√	X	√	X
C1 – 1 st generation clonal seed orchard mix (M3738)	√	√	√	√	√
C2 – 2 nd generation clonal seed orchard mix (M3870)	√	√	√	√	√
C3 – unimproved collection from commercial stand (P10005)	X	X	√	X	√
C4 – unimproved collection from commercial stand (P10007)	√	√	√	√	√

Table 4.4.2: Location and site details for all 5 tests in the ICFR progeny series.

Locality	Province	Lat.	Long.	Alt. (m)	M.A.P.(mm)	M.A.T.(°C)
Graskop	Mpumalanga	24°47'	30°52'	1583	1530	15.6
Helvetia	Mpumalanga	25°32'	30°22'	1672	737	14.9
Usutu	Swaziland	26°26'	30°59'	1388	947	16.1
Bulwer	KZN	29°51'	29°42'	1620	983	14.4
Ugie	N.E.Cape	31°11'	28°11'	1320	732	15.1

Table 4.4.3: Trial assessment and management details

Trial Locality	Previous crop	Planted	Assessments in 2000 Dbh & Heights	Site preparation and history
Graskop	<i>P. patula</i>	29.11.94	6 & 7 November	Pitted before planting; sporadic damage to trees from debarking due to baboons has occurred.
Helvetia	<i>E. fraxinoides</i>	21.10.94	29 June & 27 September	Pitted before planting; Large brush piles were present from residue of previous <i>Eucalytus</i> crop
Usutu	<i>P. patula</i>	16.11.94	5 July & 10 September	Pitted before planting
Bulwer	Unplanted grassland	19.12.94	18 October & 14 November	Site was ripped on the contour; Snow storm in the winter of 1997 caused damage to tops and branches
Ugie	Unplanted grassland	23.11.94	27 & 28 November	Site was ripped and planted to a pine crop that was destroyed by fire soon after planting, when trees were around 90cm tall. This trial was then planted onto this site soon after this event.

4.4.2 Single, paired and multiple-site analyses

4.4.2.1 Single-site analysis

In the single-site analysis the genetic checks/mixed seedlots were excluded from the data and the MIXED procedure in SAS was used to estimate variance components. In this analysis the following linear model was used:-

$$y_{ijkl} = \mu + R_i + B(R)_{ij} + F_k + F^*R_{ik} + \epsilon_{ijkl}$$

where,

y_{ijkl} = phenotypic observation for the $ijkl^{\text{th}}$ tree,

μ = trial mean

R_i = fixed effect of the i^{th} rep,

$B(R)_{ij}$ = fixed effect of the j^{th} block in the i^{th} rep,

F_k = random effect of the k^{th} family, $E[F_k] = 0$, $\text{Var}[F_k] = \sigma_F^2$,

F^*R_{ik} = random effect of the interaction between the k^{th} family and i^{th} rep, $E[r_{ik}] = 0$, $\text{Var}[r_{ik}] = \sigma_r^2$,

ϵ_{ijkl} = random error term associated with the $ijkl^{\text{th}}$ tree, $E[\epsilon_{ijkl}] = 0$, $\text{Var}[\epsilon_{ijkl}] = \sigma_e^2$

Single-site (or biased) heritability was estimated for volume/tree, for each site, using the formula:

$$h_b^2 = \frac{4 \sigma_F^2}{\sigma_T^2}$$

where $\sigma_T^2 = \sigma_F^2 + \sigma_r^2 + \sigma_e^2$ (σ_T^2 represents the phenotypic variance)

and $\sigma_F^2 = \sigma_f^2 + \sigma_{fe}^2$ where σ_f^2 and σ_{fe}^2 are the family and family x environment interaction variances in a multiple-site model (Hodge and White, 1992). The family variance was multiplied by a coefficient of 4, to give an estimate of the additive genetic variance. The single site heritability estimates from this analysis are presented in table 4.4.5.

4.4.2.2 Paired-site and multiple-site analysis

Paired-site analyses were performed for all pairs of trials in a similar way to that described previously. The linear model for these analyses was

$$y_{ijklm} = \mu + T_i + R(T)_{ij} + B(R)_{jk} + F_l + F^*T_{il} + F^*R(T)_{ijl} + \epsilon_{ijklm}$$

where,

y_{ijklm} = phenotypic observation for the $ijklm^{\text{th}}$ tree,

μ = overall mean

T_i = fixed effect of the i^{th} trial

$R(T)_{ij}$ = fixed effect of the j^{th} rep in the i^{th} trial

$B(R)_{jk}$ = fixed effect of the k^{th} block in the j^{th} rep

F_l = random effect of the l^{th} family, $E[F_l] = 0$, $\text{Var}[F_l] = \sigma_f^2$,

F^*T_{il} = random effect of the interaction between the l^{th} family and i^{th} trial, $E[r_{il}] = 0$, $\text{Var}[r_{il}] = \sigma_{fe}^2$,

$F^*R(T)_{ijl}$ = random effect of the interaction between the l^{th} family and j^{th} rep within the i^{th} trial, $E[r_{ijl}] = 0$, $\text{Var}[r_{ijl}] = \sigma_r^2$,

ϵ_{ijklm} = random error term associated with the $ijklm^{\text{th}}$ tree, $E[\epsilon_{ijklm}] = 0$, $\text{Var}[\epsilon_{ijklm}] = \sigma_e^2$

For each pair of tests, estimates of Type B genetic correlations at the family level (r_{Bg}) were calculated as follows:

$$r_{Bg} = \frac{\sigma_f^2}{\sigma_f^2 + \sigma_{fe}^2}$$

Type B genetic correlation estimates are presented in table 4.4.5.

Table 4.4.4: Single-site (h^2) heritability estimates for diameter at breast height (D6), total tree height (H6), height / diameter ratio (HD6) and volume per tree (V6) at 6 years of age in the ICFR GxE trials.

Trait	Test					Mean	Range
	Graskop	Helvetia	Usutu	Bulwer	Ugie		
D6	0.21	0.14	0.34	0.25	0.38	0.26	0.14 – 0.38
H6	0.17	0.25	0.41	0.00	0.21	0.21	0.00 – 0.41
HD6	0.26	0.23	0.19	0.09	0.29	0.21	0.09 – 0.29
V6	0.21	0.17	0.43	0.18	0.38	0.27	0.17 – 0.43

Table 4.4.5: Type B genetic correlation estimates for all pairs of tests for diameter at breast height (D6), total tree height (H6), height / diameter ratio (HD6) and volume per tree (V6) at 6 years of age in the ICFR trials series.

Paired sites					
Test1	Test2	D6	H6	HD6	V6
Bulwer	Graskop	1.00	1.00	0.34	1.00
Bulwer	Helvetia	1.00	0.79	0.58	1.00
Bulwer	Ugie	0.97	1.00	0.54	1.00
Bulwer	Usutu	0.81	0.62	0.44	0.81
Graskop	Helvetia	0.63	1.00	0.69	0.75
Ugie	Graskop	0.56	0.56	0.54	0.40
Ugie	Helvetia	0.97	0.62	0.82	0.94
Usutu	Graskop	0.88	0.84	1.00	1.00
Usutu	Helvetia	0.57	0.61	0.97	0.57
Usutu	Ugie	0.50	0.28	0.88	0.38
	Mean	0.79	0.73	0.68	0.79
	Minimum	0.50	0.28	0.34	0.38
	Maximum	1.00	1.00	1.00	1.00

Table 4.4.6: The proportions of the variance components for the family effects and their interactions at 6 years for volume in the ICFR trial series, analyzed across all tests.

Parameters estimated	Proportions	6-year data
Family / Family + Family x Environment*	$\sigma_f^2 / \sigma_f^2 + \sigma_{fe}^2$	0.83
Family x Environment / Family	$\sigma_{fe}^2 / \sigma_f^2$	0.20

*Refers to the ratio of family variance over the family and family x environment variance – this is equivalent to a Type B genetic correlation from a paired site analysis.

4.4.3 Discussion

Single-site heritability estimates calculated for all tests generally ranged between 0 and 0.43 for all traits at 5 of age (Table 4.4.4). A single-site heritability of at least 0.05 for both pairs of tests was considered to be a minimum requirement necessary to calculate Type B genetic correlations (Hodge and Dvorak, 1999). The estimates for volume were between 0.17 and 0.43. There did

not appear to be any clear trends between single-site heritability estimates amongst the other traits assessed. The only exception to the above was the height / diameter ratios where in some trials the heritability estimates are lower than for the other traits.

The overall Type B genetic correlations varied between 0.38 and 1.00 with an average of 0.79. Similar trends amongst the other growth traits were apparent (Table 4.4.5). The height to diameter ratios exhibited levels of GxE similar to the other growth traits.

The overall ratio of GxE variance to genetic variance for volume at 6 years varies was low at 0.20 (Table 4.4.6). The estimates of the ratios of genetic to genetic plus GxE when analyzed across all sites was 0.83 compared to an average Type B genetic correlation estimate of 0.79 (see Table 4.4.5 & 4.4.6). The slight discrepancy is likely to be due to the fact that the data was not standardized before analysis.

4.5 Analysis of a Sappi progeny trial series in Southern Africa

4.5.1 Introduction and Methods

4.5.1.1 Sappi Forest Research planted a series of *P. patula* progeny trials during 1996 and 1997 in order to test a combination of first and second generation OP families from its own orchards as well as some good performers from other breeding programs in the sub-region. The trials were planted over a range of site types in part also to attempt to address the question of GxE.

4.5.1.2 Description of genotypes and test site details

A total of 9 tests were established. An identical set of common second-generation OP families from Sappi's main clonal seed orchard were incorporated in all 9 tests. In addition, the trials included various other OP families from other breeding programs in Southern Africa or other clone bank / seed orchards from the Sappi breeding program. Details of the composition and nature of the tests is provided in table 4.5.1. A matrix of the number of common treatments in each of a pair of trials is presented in table 4.5.2.

4.5.1.3 Trial design, management and site details

The 9 tests were established over a period of 2 years, 4 during 1996 and 5 in the following year. These sites ranged from Elandshoogte in the north, in Mpumalanga province, through Swaziland to Epsom in KZN, in the south. Further details of the exact position and climatic characteristics of the 9 trials are provided in table 4.5.3.

All 9 trials were planted as alpha lattice designs with either 5 or 6 replications and varying number of treatments per trial (Table 4.5.1). The plot size was a 5 tree line plot and all trees were planted at stocking of between 1500 - 1800 stems per hectare. A row of trees, with similar composition to the trial, was planted around each trial as surrounds. All seedlings were raised at the Sappi Ngodwana nursery in Mpumalanga. 4 tests (PG028 – 31T) were planted in 1996 and the other 5 during 1997. No thinning had been carried out in any of the tests.

4.5.1.4 Trial assessment and data preparation

All trials, with the exception of R208, were assessed for both height and dbh (diameter at breast height, i.e. 1.3m, in cm) at either 4 or 5 years of age. The 4 tests planted in 1996 (PG28 – 31T) were assessed at 5 years while the rest were assessed at 4 years of age. Trial R208 has only been assessed for height not dbh. Although no formal crown or stem form assessments were made, any defects or abnormalities such as broken tops, forking or foxtailing were noted. The height and DBH measurements were used to calculate volume per tree, in m³ / tree, overbark, using the two methods outlined previously (see 4.2.2.1).

Table 4.5.1: Trial composition for the 9 tests in the Sappi series.

Origin of treatments	PG028T	PG029T	PG030T	PG031T	PG033T	PG035T	R208	PG034T	PG036T
Selected 2nd generation OP families - Sappi CSO	33	31	29	25	35	35	34	35	35
2nd generation OP families – Sappi other	10	9	5	2	2	75	74	2	75
2nd generation OP families – CSIR	10	10	10	10	0	0	6	0	0
2nd generation OP families – Mondi	6	6	6	6	0	0	0	0	0
1st generation OP families – Sappi	0	0	0	0	56	1	3	55	1
1st generation OP families – Zimbabwe Forestry Commission	7	7	7	7	7	7	7	7	7
2nd generation OP family orchard mix	2	2	2	2	2	2	2	2	2
1st generation OP family orchard mix	1	1	1	1	1	1	1	1	1
Unimproved seedlots	2	2	2	2	0	0	0	0	0
Total nr. of treatments	83	80	74	67	102	120	125	101	120

Table 4.5.2: Number of individual OP families* common to each pair of trials in all 9 tests of the Sappi progeny trial series.

	PG028T	PG029T	PG030T	PG031T	PG033T	PG035T	R 208	PG034T	PG036T
PG028T	71	68	62	55	37	38	43	37	38
PG029T	*	68	62	55	35	36	41	35	36
PG030T	*	*	62	55	34	34	40	34	34
PG031T	*	*	*	55	29	29	35	29	29
PG033T	*	*	*	*	99	44	45	98	44
PG035T	*	*	*	*	*	117	114	44	117
R 208	*	*	*	*	*	*	123	45	114
PG034T	*	*	*	*	*	*	*	98	44
PG036T	*	*	*	*	*	*	*	*	117

*Only includes OP families used in the single and paired site analyses

Table 4.5.3: Location and site details for all 9 tests in the Sappi progeny series.

Test	Province	Plantation	Latitude	Longitude	Altitude(m)	M.A.P. (mm)	M.A.T.(°C)
PG028T	Mpumalanga	Elandshoogte A44a	25.520	30.438	1932	912	13.9
PG033T	Mpumalanga	Helvetia E35	25.568	30.304	1672	900	15.2
PG035T	Mpumalanga	Helvetia E35	25.568	30.304	1672	900	15.2
R208	Swaziland	Usutu B18	26.435	30.947	1553	1093	14.9
PG029T	Mpumalanga	Lothair M64	26.435	30.687	1628	920	14.8
PG030T	Mpumalanga	Hlelo C54	26.988	30.630	1322	866	16.6
PG034T	KZN	Pinewoods 45a	29.619	30.095	1584	900	15.2
PG036T	KZN	Pinewoods 45a	29.619	30.095	1584	900	15.2
PG031T	KZN	Epsom B27	29.912	29.801	1415	980	14.5

4.5.2 Single, paired and multiple-site analysis

4.5.2.1 Single-site analysis

In the single-site analysis the genetic checks were excluded from the data and the MIXED procedure was used to estimate variance components. In this analysis the linear model used and single-site heritability was estimated in a similar fashion to 4.4.2.1.

4.5.2.2 Paired and multiple site analysis

Paired site analyses were performed for all pairs of trials in a similar way to that described in 4.4.2.2.

Table 4.5.4: Single-site heritability estimates for diameter at breast height (D), total tree height (H), height / diameter ratio (HD) and volume per tree (V) at 4/5 years of age in the Sappi progeny trial series.

Test												
Trait	PG028	PG029	PG030	PG031	PG033	PG035	R208**	PG034	PG036	Mean	Range	
D*	0.34	0.16	0.16	0.03	0.17	0.10	*	0.00	0.21	0.15	0.00 – 0.34	0.34
H*	0.28	0.10	0.24	0.00	0.22	0.18	0.27	0.13	0.25	0.18	0.00 – 0.28	0.28
HD*	0.13	0.10	0.12	0.07	0.08	0.07	*	0.00	0.10	0.08	0.00 – 0.13	0.13
V*	0.38	0.16	0.22	0.05	0.24	0.14	*	0.07	0.25	0.19	0.05 – 0.38	0.38

*The assessments reflect 2 different ages (4 & 5 years of age) – depending on trial.

**Only tree height was measured in this test.

Table 4.5.5: Type B genetic correlation estimates for all pairs of tests for diameter at breast height (D), total tree height (H), height / diameter ratio (HD) and volume per tree (V) at 4 /5 years of age in the Sappi progeny trial series.

Paired Sites		D*	H*	HD*	V*
Test1	Test2	r _{Bg}	r _{Bg}	r _{Bg}	r _{Bg}
PG028T	PG029T	0.51	0.50	0.93	0.39
PG028T	PG030T	0.73	0.40	0.78	0.65
PG028T	PG031T	1.00	0.34	0.92	0.72
PG028T	PG033T	0.55	0.52	0.62	0.31
PG028T	PG035T	1.00	0.61	1.00	0.40
PG028T	R208**	*	0.42	*	*
PG028T	PG034T	1.00	0.83	1.00	0.33
PG028T	PG036T	0.44	0.67	0.47	0.23
PG029T	PG030T	0.44	0.01	0.78	0.16
PG029T	PG031T	1.00	0.07	1.00	0.73
PG029T	PG033T	0.25	0.40	0.85	0.10
PG029T	PG035T	0.27	0.63	0.85	0.15
PG029T	R208**	*	0.56	*	*
PG029T	PG034T	0.72	0.38	1.00	0.13
PG029T	PG036T	0.73	0.63	0.69	0.45
PG030T	PG031T	0.61	0.48	1.00	0.27
PG030T	PG033T	0.90	0.55	1.00	0.30
PG030T	PG035T	0.57	0.55	0.81	0.18
PG030T	R208**	*	0.67	*	*
PG030T	PG034T	1.00	1.00	1.00	0.25
PG030T	PG036T	0.55	0.32	0.50	0.21
PG031T	PG033T	0.00	0.00	0.00	0.00
PG031T	PG035T	0.00	0.00	0.51	0.00
PG031T	R208**	*	0.54	*	*
PG031T	PG034T	1.00	1.00	1.00	1.00
PG031T	PG036T	0.89	1.00	0.13	1.00
PG033T	PG035T	1.00	0.77	1.00	0.96
PG033T	R208**	*	1.00	*	*
PG033T	PG034T	0.74	0.71	1.00	0.57
PG033T	PG036T	0.28	0.45	0.91	0.36
PG035T	R208**	*	0.84	*	*
PG035T	PG034T	1.00	1.00	1.00	1.00
PG035T	PG036T	0.75	0.73	0.38	0.95
R208**	PG034T	*	0.93	*	*
R208**	PG036T	*	0.75	*	*
PG034T	PG036T	0.82	1.00	0.00	0.84
	Mean	0.67	0.59	0.75	0.45
	Minimum	0.00	0.00	0.00	0.00
	Maximum	1.00	1.00	1.00	1.00

**In R208 only heights were assessed.

Table 4.5.6: The proportions of the variance components for the family effects and their interactions at 5 years in the S1 and 4 years in the S2** Sappi trial series, analyzed across all 4 tests in each series.**

Parameters estimated	Proportions	5-year data (S1)	4-year data (S2)
Family / Family + Family x Environment*	$\sigma_f^2 / \sigma_f^2 + \sigma_{fe}^2$	0.48	0.82
Family x Environment / Family	$\sigma_{fe}^2 / \sigma_f^2$	1.09	0.22

*Refers to the ratio of family variance over the family and family x environment variance – this is equivalent to a Type B genetic correlation from a paired site analysis.

**S1 = PG28, 29, 30, 31 and S2 = PG33, 34, 35, 36.

4.5.3 Discussion

Single-site heritability estimates calculated for all tests generally ranged between 0 and 0.38 for all traits at 5 years of age (Table 4.5.4). A single-site heritability of at least 0.05 for both pairs of tests was considered to be a minimum requirement necessary to calculate Type B genetic correlations (Hodge and Dvorak, 1999). The estimates for volume were between 0.05 and 0.38. There did not appear to be any clear trends between single-site heritability estimates amongst the other traits assessed. The only exception to the above was the height / diameter ratios where in some trials the heritability estimates were lower than for the other traits.

The overall Type B genetic correlations for volume varied between 0 and 1.00 with an average of 0.45. Similar trends amongst the other growth traits were apparent (Table 4.5.5), although the correlations were slightly higher. The height to diameter ratios (HD) exhibited lower levels of GxE than the other growth traits.

The overall ratio of GxE variance to genetic variance for volume at 4 or 5 years varies was high at 1.09 for series S1 and low 0.22 for S2 (Table 4.5.6). The reason for the large difference in estimates is likely to be related to the sampling of environments in each series. In S1 there are 4 widely spread sites whereas in S2 there were only two sites with two tests at each site. The estimates of the ratios of genetic to genetic plus GxE variances when analyzed across all sites was 0.48 for S1 and 0.82 for S2 compared to an average Type B genetic correlation estimate of 0.45 (see Table 4.5.5 & 4.5.6). However, here again the average of the pairs only within series S1 was 0.49.

4.6 General discussion and conclusions

4.1.1 A considerable number of Type B genetic correlations were estimated and there were considerable differences in estimates of single site heritabilities amongst sites. The opportunity

was thus presented to compare the estimates of heritability and Type B genetic correlations and determine if any relationship exists. Indeed it has been previously reported that higher heritabilities were associated with higher Type B genetic correlations (Johnson, 1997). The comparison was done for all the estimates using volume at 5 years and the relationship is presented in figure 4.6.1. The phenotypic correlation between these two estimates was 0.01.

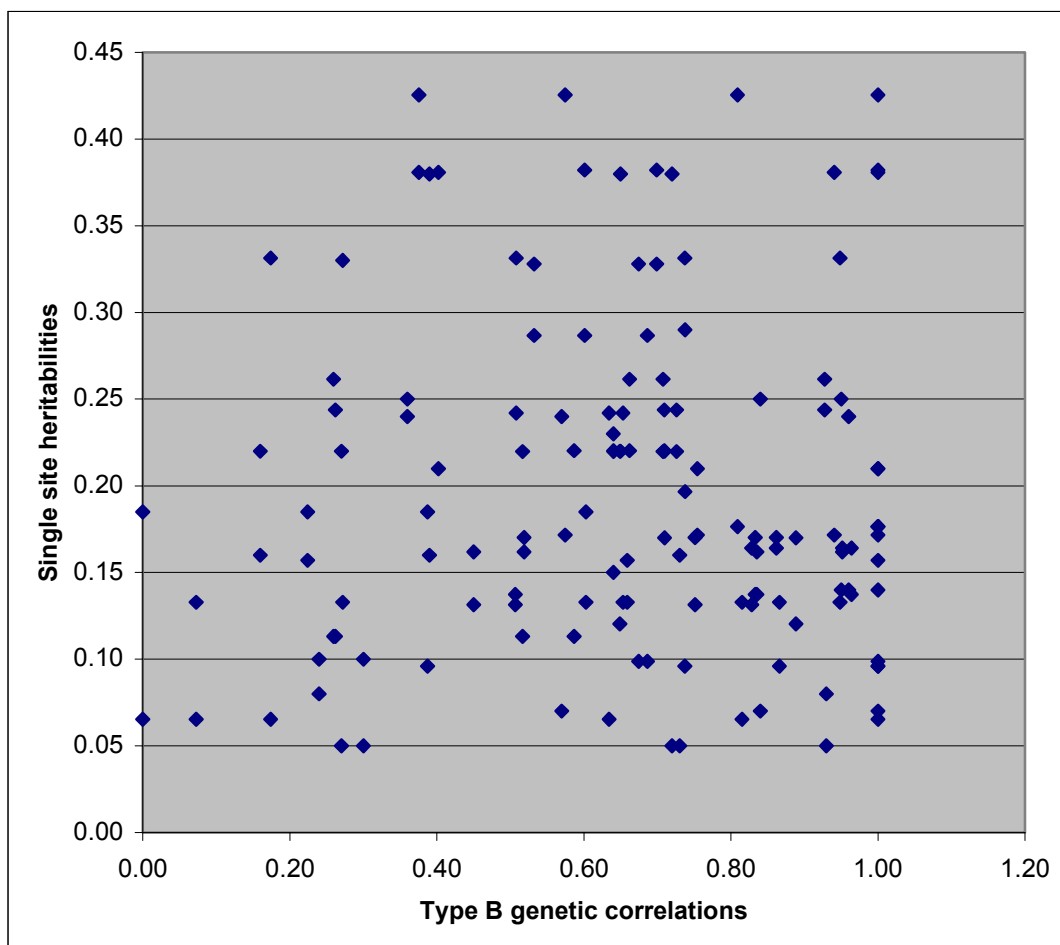


Figure 4.6.1: The relationship between heritability and type B genetic correlations for all pairs of sites with heritabilities estimated for volume at 5 years.

4.1.2 There does not appear to be any obvious linear relationship between the two estimates. This is reassuring because the Type B Genetic correlations should respond to environment without being severely influenced by heritability. On the other hand, one would expect that less clear genetic differences in any test should have an effect on the precision of their interaction.

4.1.3 The suspicion that GxE may be important in Southern Africa for *P. patula* has been reported for a number of years (Denison, 1973), (Falkenhagen, 1979), (Barnes et al., 1992), (Snedden and Verryin, 1999). However, none of the previous studies, with the exception of the

last mentioned one, went any further than reporting its presence. The latter study (Snedden and Verryn, 1999), suggested some responses for breeding the species but only really looked at the Mpumalanga region of South Africa.

4.1.4 In this study, the entire region encompassing South Africa and Swaziland was considered. A large number of provenance and progeny tests were available for analysis. The exact number of tests, origin and structure, and sites are summarized in table 4.6.1. The material available encompassed a broad sample of the entire region, utilizing 65 tests on 42 sites. In addition, the tests included representative populations from almost the entire range of the populations in Mexico as well as material originating and selected from the South African land race. The latter tests included both first and second-generation open-pollinated families. It should be noted however, that no single genotype was common to all tests, and indeed each trial series seldom included more than 10 tests.

Table 4.6.1: A summary of the tests utilized in this chapter to determine the amount GxE in Southern Africa, including details of the number of tests and sites, as well as a brief description of origin.

Origin	Age	Nr. of tests	Nr. of sites	Description
CAMCORE	3-8	43	22	Provenance/progeny tests including collections from a broad sample of the entire range of <i>P. patula</i> in Mexico.
FAO – Oxford	8-10	8	8	Provenance tests including some similar material as CAMCORE collected from Mexico but not including family structure.
ICFR	6	5	5	Open-pollinated 1 st gen. families selected from the South African land race in KZN.
Sappi	4-5	9	7	Open-pollinated 2 nd gen. Families selected from the South African land race in Mpumalanga.
		Total 65	42	

4.1.5 The amount of GxE present overall was quantified and in addition, the material available gave some opportunity for comparing the GxE across different populations and between the Mexican and South African material. It has been suggested that where the GxE interaction variance is 50% or more of the genetic component, the effects of the GxE interaction are likely to be serious on gains from selection and breeding (Shelbourne, 1972). In terms of the parameter used to estimate GxE in this chapter, this represents an $r_{Bg} = 0.67$.

4.1.6 The overall mean Type B genetic correlation estimate for all tests across all sites was 0.62 (Table 4.6.2). These estimates were however done without standardization and perhaps a more meaningful estimate should exclude the effects of heterogeneous variances. This is considered in the following chapter.

Table 4.6.2: Mean Type B genetic correlations for all 5 growth traits (H = tree height, D = diameter at breast 1.3m, HD = height over diameter ratio; V = volume per tree) for each trial series.

Trial series	Age	Pairs	D	H	HD	V	Description
CAMCORE s0104	5	13	0.72	0.73	0.73	0.75	Provenances originate from the central area of the distribution of <i>P. patula</i> in Mexico. <i>Pinus patula</i> var. <i>patula</i>
	8	9	0.67	0.61	0.81	0.60	
CAMCORE s0203	5	7	0.66	0.71	0.56	0.70	Provenances originate from the southern area of the distribution of <i>P. patula</i> in Mexico. <i>Pinus patula</i> var. <i>longipedunculata</i>
	8	4	0.31	0.60	0.75	0.46	
CAMCORE s05-07	5	27	0.63	0.64	0.71	0.58	Provenances originate mainly from northern to central area of distribution of <i>P. patula</i> in Mexico. <i>Pinus patula</i> var. <i>patula</i>
	8	10	0.81	0.78	0.93	0.70	
CAMCORE s0809	5	4	0.60	0.58	0.81	0.53	Provenances originate from the northern to central area of distribution of <i>P. patula</i> in Mexico. <i>Pinus patula</i> var. <i>patula</i>
CAMCORE s15	5	1	0.73	0.74	0.64	0.63	Provenances originate from the central area of distribution of <i>P. patula</i> in Mexico. <i>Pinus patula</i> var. <i>patula</i>
ICFR	6	10	0.79	0.73	0.68	0.79	Families originate from selections in unimproved plantations of South African landrace material. Likely to be mainly <i>Pinus patula</i> var. <i>patula</i>
SAPPI	4/5	36	0.67	0.59	0.75	0.45	Families originate from in most cases 2 nd generation selections in SA breeding populations. Likely to be mainly <i>Pinus patula</i> var. <i>patula</i>
Mean			0.66	0.67	0.74	0.62	
Minimum			0.31	0.58	0.56	0.45	
Maximum			0.81	0.78	0.93	0.79	

4.1.7 The overall mean, given above, can however, be very misleading as they mask the variation between populations which may in fact be far more interesting and revealing than the mean. Amongst the Mexican imported material considerable variation in GxE exists. The material from the southern and central parts of the distribution of *P. patula* in Mexico generally exhibited less GxE than the northern material. The northern material was tested in trial series 05, 06, 07, 08 and 09. The northern provenances represented in these series include Conrado Castillo, El Cielo, Pinal de Amoles, La Encarnacion and Zacualtipan. The actual interactions were looked at in more detail in the following chapter.

4.1.8 Comparing the amount of GxE for the imported Mexican and South African material, reveals little difference overall. The CAMCORE average was 0.68 and the South African material 0.70. This is perhaps a little surprising because the expectation would be that the imported Mexican material would be more interactive. Amongst the South African material the Sappi families were most interactive and this may in fact be a reflection of the environments sampled. Considerable differences between the sites in this series exist.

CHAPTER 5 – IDENTIFICATION OF THE PATTERNS AND STATISTICAL CAUSES THAT CONTRIBUTE TO THE GxE VARIANCE

Chapter Summary

5.1 Introduction

5.2 Impact of heterogeneous variances on the GxE variance

5.3 The distribution of the GxE variance across sites

5.4 An investigation into the genotypic response using the joint regression analysis

5.4 An examination of actual rank changes amongst genotypes

5.5 Differences in response amongst different populations across similar environments

5.1 Introduction

The previous chapter clearly indicated that some GxE was present within *P. patula* in Southern Africa. Both the ANOVA and type B genetic correlations have given some measure of the extent of this GxE. However, statistically significant interaction may be caused by several factors, including heterogeneity of variance among tests, the genotypes varying in their responses and actual variations that lead to rank changes. The nature of the interaction will have an important bearing on the strategy adopted for the species in the sub-region. In addition, even if significant rank changes can be identified, a quantification of the numbers of genotypes or alternatively environments responsible for these interactions is also important. The objective of this chapter is thus to determine the nature of the interaction variance and quantify the extent of these interactions amongst genotypes and environments.

5.2 The impact of heterogeneous variances on the GxE variance

5.2.1 Introduction

5.2.1.1 It is important in the first instance to distinguish between interactions due to heterogeneity of genotypic variance, from those due to a lack of correlation of genotypic performance among environments (Cooper and DeLacy, 1994). The former should be quantified and eliminated before considering the latter interactions (Lefkovitch, 1990). In this section the data is analysed with and without standardizing the data and differences compared.

5.2.2 The standardization of data

All genetic checks were excluded from the data before analysis. Identical ANOVA's were performed in each case using both unstandardized(u) and standardized(s) data. The data was standardized using the STANDARD procedure in SAS. The data for each test was standardized to a mean of 0 and a standard deviation of 1. The standardization was done by test so that each test could be fairly compared.

5.2.3 The impact of standardizing data on paired site analysis

5.2.3.1 All the Type B genetic correlations estimated in the preceding chapter were done with unstandardized data. These Type B genetic correlations were used to quantify over the amount of GxE present over the range of sites sampled. In this section the effect of heterogeneity of

variances on the GxE estimates is quantified by comparing the analyses with both standardized and unstandardized data. Standardization was done in the same manner as before.

5.2.3.2 Standardized and unstandardized data analysis using selected CAMCORE tests.

The Type B genetic correlations for pairs of tests in the CAMCORE series 01, 02, 05, 06, 07 series were calculated using both standardized and unstandardized data. The estimated Type B genetic correlations for both data sets are presented in table 5.2.1.

5.2.3.3 Standardized and unstandardized data analysis using the ICFR and Sappi progeny tests.

The Type B genetic correlations for pairs of tests in the ICFR and Sappi progeny trial series were calculated using both standardized and unstandardized data. The estimated Type B genetic correlations for both data sets are presented in tables 5.2.2 and 5.2.3.

5.2.4 Discussion on the impact of standardizing data on the GxE variance

5.2.4.1 On the whole, the differences in the estimates of the Type B genetic correlations between using unstandardized and standardized was not large (Table 5.2.1, 5.2.1 & 5.2.3). In many cases, for example in CAMCORE series 01, 02 and 07 there was no appreciable difference overall, whereas in other cases the mean estimates increased in most instances. The expectation would be that GxE would be inflated by heterogenous variances so that the GxE variance should decrease (and thus Type B genetic correlation estimates increase) using standardized data. In the ICFR trial series the mean estimate actually decreased which was unexpected. A two-tailed, paired-observation test for significant differences between pairs for all the CAMCORE material, the ICFR and the Sappi tests suggested that the differences were sometimes, but not in all cases, significant.

5.2.4.2 There appears to be a trend for increased discrepancies amongst the estimates, with increasing growth differences between pairs of sites. One example of this is the comparison between estimates of Type B genetic correlations between tests in the Sappi series (Table 5.2.3). Generally large differences in the estimates are apparent when comparing Type B genetic correlations for pairs of tests between Sappi series 1 (PG 28 – 31) and 2 (PG33 – 36). The differences in growth are particularly large because assessments were made at 5 and 4 years respectively. In this case it would be essential to standardize the data before assessing for GxE.

This apparent relationship was examined in more detail by plotting the absolute difference in volume growth between each pair of sites and the difference between the standardized and unstandardized Type B genetic correlation estimates (Figure 5.2.1). The phenotypic correlation

between these two variables was 0.53. It would thus seem apparent that the impact of standardization became more important the greater the absolute difference in growth.

Table 5.2.1: Estimates using both unstandardized and standardized data for type B Genetic, Provenance and aggregate family-provenance correlations for all pairs of tests for volume per tree at 5 years of age in CAMCORE trial series 01, 02, 05, 06, & 07.

Paired Sites		CAMCORE series 01					
Test1	Test2	rBg(u)	rBg(s)	rBp(u)	rBp(s)	rBg*(u)	rBg*(s)
20-10-01A	20-10-01B	0.80	0.84	1.00	0.98	0.83	0.86
20-10-01A	20-18-01H	0.69	0.82	0.06	0.00	0.50	0.48
20-10-01A	20-07-01L	0.79	0.80	0.66	0.61	0.75	0.74
20-10-01A	20-18-01J	0.50	0.53	0.03	0.01	0.44	0.47
20-10-01B	20-18-01H	1.00	1.00	0.87	0.81	0.96	0.95
20-10-01B	20-07-01L	0.73	0.74	1.00	1.00	0.86	0.89
20-10-01B	20-18-01J	0.94	0.94	0.99	0.99	0.94	0.94
20-18-01H	20-07-01L	0.71	0.80	1.00	0.90	0.83	0.84
20-18-01H	20-18-01J	0.98	1.00	0.56	0.49	0.83	0.80
20-07-01L	20-18-01J	0.44	0.45	0.85	0.97	0.52	0.55
	Mean	0.76	0.79	0.70	0.68	0.75	0.75
	Minimum	0.44	0.45	0.03	0.00	0.44	0.47
	Maximum	1.00	1.00	1.00	1.00	0.96	0.95
		CAMCORE series 02					
20-10-02A	20-10-02B	0.98	0.89	1.00	1.00	1.00	0.97
20-10-02A	20-07-02D	0.63	0.71	0.87	0.83	0.69	0.72
20-10-02A	20-18-02E	0.87	0.87	0.74	0.74	0.67	0.68
20-10-02B	20-07-02D	0.47	0.64	1.00	0.78	0.60	0.57
20-10-02B	20-18-02E	0.68	0.77	0.71	0.95	0.70	0.91
20-07-02D	20-18-02E	0.50	0.62	0.50	0.52	0.53	0.47
	Mean	0.69	0.75	0.80	0.80	0.70	0.72
	Minimum	0.47	0.62	0.50	0.52	0.53	0.47
	Maximum	0.98	0.89	1.00	1.00	1.00	0.97
		CAMCORE series 05					
20-10-05F	20-10-05E1	0.72	0.77	0.75	0.99	0.71	0.80
20-10-05F	20-10-05E2	0.36	0.61	0.00	0.00	0.26	0.51
20-10-05F	20-07-05L	0.89	0.88	1.00	1.00	0.93	0.92
20-10-05F	20-18-05K	0.77	0.79	0.31	0.58	0.73	0.77
20-10-05E1	20-10-05E2	0.63	0.80	0.40	0.00	0.59	0.76
20-10-05E1	20-07-05L	0.65	0.71	0.83	0.93	0.66	0.74
20-10-05E1	20-18-05K	0.74	0.74	0.00	0.00	0.64	0.65
20-10-05E2	20-07-05L	0.38	0.67	0.04	0.00	0.26	0.49
20-10-05E2	20-18-05K	0.62	0.87	0.00	0.00	0.52	0.77
20-07-05L	20-18-05K	0.73	0.77	0.58	0.70	0.71	0.76
	Mean	0.65	0.76	0.39	0.42	0.60	0.72
	Minimum	0.36	0.61	0.00	0.00	0.26	0.49
	Maximum	0.89	0.88	1.00	1.00	0.93	0.92

Table 5.2.1 continued.....

		CAMCORE series 06					
20-10-06B1	20-10-06B2	0.77	0.71	0.88	0.92	0.82	0.75
20-10-06B1	20-07-06E	0.32	0.53	0.00	0.00	0.17	0.28
20-10-06B1	20-18-06D	0.71	0.81	0.32	0.32	0.63	0.69
20-10-06B2	20-07-06E	0.27	0.51	0.16	0.49	0.27	0.54
20-10-06B2	20-18-06D	0.55	0.71	1.00	1.00	0.65	0.80
20-07-06E	20-18-06D	0.51	0.59	0.57	0.72	0.51	0.60
	Mean	0.52	0.64	0.49	0.58	0.51	0.61
	Minimum	0.27	0.51	0.00	0.00	0.17	0.28
	Maximum	0.77	0.81	1.00	1.00	0.82	0.80
		CAMCORE series 07					
20-10-07B1	20-10-07B2	1.00	0.95	1.00	0.81	1.00	0.90
20-10-07B1	20-07-07D	0.48	0.55	0.26	0.30	0.39	0.44
20-10-07B1	20-18-07A	0.85	0.84	0.79	0.78	0.87	0.86
20-10-07B2	20-07-07D	0.60	0.78	0.00	0.00	0.22	0.27
20-10-07B2	20-18-07A	0.87	0.98	0.66	0.64	0.66	0.62
20-07-07D	20-18-07A	0.56	0.60	0.76	0.76	0.60	0.63
	Mean	0.73	0.78	0.58	0.55	0.62	0.62
	Minimum	0.48	0.55	0.00	0.00	0.22	0.27
	Maximum	1.00	0.98	1.00	0.81	1.00	0.90
	TTest	***		ns		***	

ns no significance between pairs for the paired site, 2 tailed T Test

*** Significant at >0.001 between pairs for the paired site, 2 tailed T Test

Table 5.2.2: Estimates using both unstandardized and standardized data for type B Genetic correlations for all pairs of tests for volume per tree at 6 years of age in the ICFR progeny trial series.

Paired sites			
Test1	Test2	rBg(u)	rBg(s)
Graskop	Helvetia	0.75	0.77
Graskop	Usutu	1.00	0.96
Graskop	Bulwer	1.00	1.00
Graskop	Ugie	0.40	0.45
Helvetia	Usutu	0.57	0.50
Helvetia	Bulwer	1.00	1.00
Helvetia	Ugie	0.94	0.86
Usutu	Bulwer	0.81	0.70
Usutu	Ugie	0.38	0.40
Bulwer	Ugie	1.00	0.95
	Mean	0.79	0.76
	Minimum	0.38	0.40
	Maximum	1.00	1.00
	TTest	Ns	

ns no significance between pairs for the paired site, 2 tailed T Test

Table 5.2.3: Estimates using both unstandardized and standardized data for type B Genetic correlations for all pairs of tests for volume per tree at 4/5 years of age in the Sappi progeny trial series.

Paired sites			
Test1	Test2	rBg(u)	rBg(s)
PG028	PG029	0.39	0.43
PG028	PG030	0.65	0.64
PG028	PG031	0.72	0.91
PG028	PG033	0.31	0.66
PG028	PG034	0.33	1.00
PG028	PG035	0.40	0.96
PG028	PG036	0.23	0.57
PG029	PG030	0.16	0.20
PG029	PG031	0.73	0.78
PG029	PG033	0.10	0.15
PG029	PG034	0.13	0.50
PG029	PG035	0.15	0.24
PG029	PG036	0.45	0.67
PG030	PG031	0.27	0.44
PG030	PG033	0.30	0.64
PG030	PG034	0.25	1.00
PG030	PG035	0.18	0.50
PG030	PG036	0.21	0.50
PG031	PG033	0.00	0.00
PG031	PG034	1.00	1.00
PG031	PG035	0.00	0.00
PG031	PG036	1.00	0.67
PG033	PG034	0.57	0.82
PG033	PG035	0.96	0.94
PG033	PG036	0.36	0.35
PG034	PG035	1.00	1.00
PG034	PG036	0.84	0.88
PG035	PG036	0.95	0.81
	Mean	0.45	0.62
	Minimum	0.00	0.00
	Maximum	1.00	1.00
	TTest	***	

*** Significant at >0.001 between pairs for the paired site, 2 tailed T Test

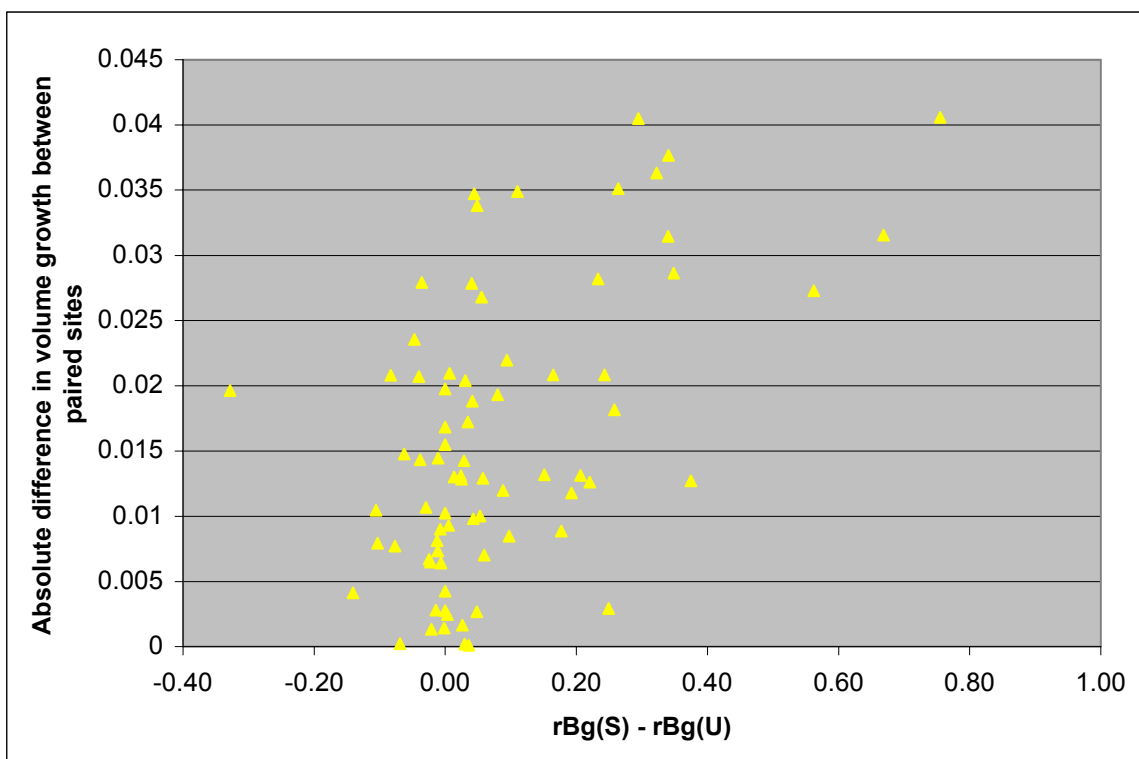


Figure 5.2.1: The relationship between the absolute difference in volume growth between pairs of sites and the difference between the standardized and unstandardized Type B genetic correlations.

5.3 The distribution of the GxE variance across sites

5.3.1 Introduction

5.3.1.1 It is appropriate when looking at GxE to consider the effect of individual environments on the GxE variance. Other studies have suggested that often the latter variance can be largely attributed to one or only a few 'interactive' environments (Woolaston et al., 1991),(Carson, 1991). The Type B genetic correlations estimated using standardized data were utilized to look at the GxE amongst sites with reference to the distribution of this GxE across sites.

5.3.2 The contribution of site to the GxE variance

5.3.2.1 The estimates of Type B genetic correlations using standardized data from the previous section were examined on a per test basis to assess the effect of environment on GxE. Results from the CAMCORE tests are presented in table 5.3.1 and for the South African material in table 5.3.2.

5.3.3 Discussion

5.3.3.1 The mean Type B genetic correlations per site do vary from 0.45 to 0.91 for the CAMCORE tests and between 0.43 and 0.91 for the South African material (Table 5.3.1 & 5.3.2). In none of the trial series can high levels of GxE (i.e. low Type B genetic correlations) be attributed to only 1 or 2 tests or sites. Generally, moderate to high GxE variance between each individual test and the others is apparent in many of the trials. A consideration of the minimum Type B genetic correlations for each test further supports this assertion. Average Type B genetic correlations of around 0.61 to 0.76 can be considered typical. A Type B genetic correlation of 0.67 corresponds to a level where the interaction component is 50% of the genetic variance. This level has significance only because this was the point at which it has been suggested that gains from selection and breeding could be negatively impacted by GxE (Shelbourne, 1972).

5.3.3.2 There are a few exceptions to above, for example the Bulwer test in the ICFR series and the Jessievale test (20-10-01B) in the CAMCORE 01 series had average Type B genetic correlation estimates of 0.91. One possible explanation might be that these tests measured the genetic differences less precisely and would thus mask 'real' Type B genetic correlations. However, in neither these two cases was the single site heritability of these tests the lowest in their respective trial series and in addition no relationship between heritability and the Type B genetic correlation was found (see chapter 4). Furthermore, no obvious environmental factor could be attributed to these exceptions.

Table 5.3.1: Mean, minimum and maximum estimates of type B genetic correlations for each test in the CAMCORE series 01, 02, 05, 06, 07.

Tests	Mean	Minimum	Maximum
20-07-01L	0.75	0.55	0.89
20-10-01B	0.91	0.86	0.95
20-18-01J	0.69	0.47	0.94
20-10-01A	0.64	0.47	0.86
20-18-01H	0.77	0.48	0.95
20-07-02D	0.59	0.47	0.72
20-18-02E	0.68	0.47	0.91
20-10-02A	0.79	0.68	0.97
20-10-02B	0.81	0.57	0.97
20-07-05L	0.73	0.49	0.92
20-10-05F	0.75	0.51	0.92
20-18-05K	0.74	0.65	0.77
20-10-05E1	0.74	0.51	0.80
20-10-05E2	0.63	0.49	0.77
20-07-06E	0.47	0.28	0.60
20-18-06D	0.70	0.60	0.80
20-10-06B1	0.57	0.28	0.75
20-10-06B2	0.70	0.54	0.80
20-07-07D	0.45	0.27	0.63
20-18-07A	0.63	0.62	0.86
20-10-07B1	0.73	0.44	0.90
20-10-07B2	0.60	0.27	0.90

Table 5.3.2: Mean, minimum and maximum estimates of type B genetic correlations for each test in the ICFR and Sappi series of progeny trials.

Test	Mean	Minimum	Maximum
Graskop	0.79	0.45	1.00
Helvetia	0.78	0.50	1.00
Usutu	0.64	0.40	0.96
Bulwer	0.91	0.70	1.00
Ugie	0.67	0.40	0.95
PG28	0.74	0.43	1.00
PG29	0.43	0.15	0.78
PG30	0.56	0.20	1.00
PG31	0.54	0.00	1.00
PG33	0.51	0.00	0.94
PG34	0.89	0.50	1.00
PG35	0.64	0.00	1.00
PG36	0.64	0.35	0.88

5.4 An investigation into the genotypic response using joint regression analysis

5.4.1 Introduction

5.4.1.1 The GxE variance after adjusting for any effects caused by heterogeneous variance between sites was still found to be substantial, with Type B genetic correlations of around 0.67. This remaining interaction variance must be associated with a lack of correlation of genotypic performance among environments (Dickerson, 1962). In particular a distinction needs to be made for those interactions which lead to changes in ranking from one environment to another (Matheson and Cotterill, 1990). This latter interaction may impede response to selection and breeding (Cooper and DeLacy, 1994). This distinction needs to be carefully assessed before any decisions can be made on how to manage the GxE identified. Joint regression analysis can be used to express the performance of the genotypes as a linear function of an environmental index (Yates and Cochran, 1938), (Finlay and Wilkinson, 1963), (Eberhart and Russel, 1966) and is utilized here to identify and quantify the proportion of interacting genotypes.

5.4.2 Regression analysis as a tool for determining the types of GxE variance

5.4.2.1 A statistical technique to compare the performance of treatments at each site was utilised (Finlay and Wilkinson, 1963). This technique has also been utilised with some success in forest crops (Morgenstein and Teich, 1969), (Gullberg and Vegerfors, 1987), (Li and McKeand, 1989), (Raymond et al., 1997). For each treatment (either at a provenance level or at a family level), common to all sites in each series, a linear regression of the individual predicted yield, at 5 years, on the mean yield of all treatments at each site was computed. This latter mean yield per site was taken as an evaluation of site quality. This technique has been criticised on statistical grounds because the environment is quantified by the mean of all genotypes growing in it (Freeman and Perkins, 1971). These authors suggested that some related genotype(s) could be used as a more appropriate measure of the environment. This was attempted by using the genetic checks present within the trial, but, in fact, these genotypes themselves were subject to GxE (see table 5.4.4, 5.4.7, 5.4.8, 5.4.9) and the regressions computed gave fundamentally the same results. The predicted yields for each treatment, in these regressions, was calculated using the least square means derived by utilising the GLM procedure in SAS. The GLM analyses were done on a per test basis and included provenance, replication and provenance x replication or family and replication in the model.

5.4.2.2 The response of each genotype to an 'environmental index' (i.e. the mean yield at each site) was estimated using the regression coefficient (b_1). The slope of the line for each genotype

was taken as an indication of this response, with $b_1 = 1$ indicating an average stability since the response of that particular genotype is parallel to the mean response of all the genotypes. Genotypes with $b_1 > 1$ are unstable but respond to higher yielding environments whereas those with $b_1 < 1$ are stable and thus relatively unresponsive to site quality. Tables and figures below are presented for each of the trial series. These give estimates of the growth of each genotype per site and across sites as well as the degree of response to the environment as measured by the regression coefficient.

5.4.2.3 Amongst CAMCORE tests the South African genetic checks have been included in the analyses and are defined as an additional 'provenance' (SA).

5.4.2.4 Joint regression analysis using the CAMCORE 01/04 series

see table 5.4.1, 5.4.2 and figures 5.4.1 and 5.4.2.

Table 5.4.1: Volume / tree (V5) for each provenance at 5 years of age, at each of 8 sites in CAMCORE series 01 & 04, estimated regression coefficients (b_1) and the coefficient of determination (R^2) for regression models. Provenances included are (1) = Potrero de Monroy, (2) = Ingenio del Rosario, (3) = Corralitla and (SA) = South African genetic checks or controls.

Prov	20-07-01L	20-07-04C	20-10-01B	20-10-04A2	20-18-01J	20-10-01A	20-18-01H	20-10-04A1	Pmean#	Rank	b_1^*	R^2
1	0.051	0.048	0.037	0.037	0.035	0.033	0.030	0.026	0.037	1	1.01	0.98
2	0.045	0.043	0.032	0.032	0.033	0.030	0.024	0.023	0.033	4	0.94	0.99
3	0.047	0.047	0.035	0.034	0.033	0.036	0.024	0.025	0.035	3	1.02	0.98
SA	0.049	0.050	0.036	0.034	0.034	0.034	0.028	0.026	0.036	2	1.03	0.99
Tmean#	0.048	0.047	0.035	0.034	0.034	0.033	0.027	0.025	0.035			

#Pmean and Tmean refer to the means of those provenances across all sites and the means of those tests across all provenances respectively.

*Regression coefficients (b_1) differs significantly from 1 (*P>0.1; **P>0.05; ***P>0.01)

Table 5.4.2: Volume / tree (V5) for each common family / seedlot at 5 years of age, at each of 5 sites in CAMCORE series 01, estimated regression coefficients (b_1) and the coefficient of determination (R^2) for regression models. Provenances included are (1) = Potrero de Monroy, (2) = Ingenio del Rosario, (3) = Corralitla and (SA) = South African genetic checks or controls.

Fam	Prov	20-07-01L	20-10-01B	20-18-01J	20-10-01A	20-18-01H	Fmean#	Rank	B_1^*	R^2
22	1	0.056	0.040	0.039	0.041	0.036	0.042	1	0.97	0.96
54	3	0.053	0.043	0.036	0.048	0.030	0.042	2	0.96	0.68
21	1	0.057	0.040	0.035	0.042	0.031	0.041	3	1.25	0.93
2	1	0.058	0.037	0.035	0.036	0.034	0.040	4	1.19	0.88
16	1	0.052	0.037	0.038	0.036	0.030	0.039	5	1.06	0.99
74	3	0.052	0.039	0.039	0.036	0.027	0.038	6	1.13	0.97
57	3	0.052	0.039	0.030	0.040	0.029	0.038	7	1.07	0.82
997	SA	0.053	0.036	0.038	0.038	0.025	0.038	8	1.25	0.97
10	1	0.051	0.040	0.037	0.030	0.033	0.038	9	0.92	0.79

Table 5.4.2 continued....

Fam	Prov	20-07-01L	20-10-01B	20-18-01J	20-10-01A	20-18-01H	Fmean#	Rank	B ₁ *	R ²
14	1	0.054	0.036	0.035	0.035	0.028	0.038	10	1.23*	0.99
27	1	0.048	0.039	0.038	0.033	0.031	0.038	11	0.77	0.90
38	2	0.047	0.033	0.040	0.041	0.027	0.038	12	0.84	0.70
67	3	0.049	0.039	0.036	0.037	0.026	0.037	13	1.06	0.95
7	1	0.049	0.039	0.037	0.029	0.031	0.037	14	0.92	0.81
999	SA	0.048	0.041	0.030	0.036	0.030	0.037	15	0.87	0.80
6	1	0.049	0.036	0.037	0.031	0.031	0.037	16	0.90	0.90
12	1	0.051	0.031	0.032	0.034	0.032	0.036	17	0.99	0.81
9	1	0.051	0.036	0.034	0.028	0.030	0.036	18	1.08	0.84
50	2	0.048	0.035	0.035	0.034	0.027	0.036	19	0.95	1.00
45	2	0.051	0.034	0.036	0.032	0.025	0.036	20	1.22	0.98
5	1	0.044	0.035	0.037	0.033	0.029	0.036	21	0.66**	0.92
8	1	0.050	0.037	0.035	0.028	0.028	0.036	22	1.09	0.88
41	2	0.048	0.033	0.034	0.037	0.026	0.036	23	0.98	0.95
11	1	0.048	0.037	0.034	0.029	0.029	0.035	24	0.96	0.89
66	3	0.048	0.036	0.034	0.031	0.028	0.035	25	0.98	0.97
26	1	0.053	0.037	0.028	0.033	0.026	0.035	26	1.30	0.92
62	3	0.043	0.038	0.030	0.035	0.025	0.034	27	0.82	0.80
69	3	0.050	0.035	0.034	0.031	0.023	0.034	28	1.24*	0.99
55	3	0.042	0.033	0.034	0.040	0.023	0.034	29	0.79	0.65
48	2	0.047	0.033	0.032	0.035	0.025	0.034	30	1.00	0.96
73	3	0.051	0.030	0.031	0.036	0.022	0.034	31	1.36	0.94
64	3	0.048	0.032	0.031	0.035	0.023	0.034	32	1.13	0.96
71	3	0.045	0.032	0.033	0.035	0.023	0.034	33	0.98	0.94
53	2	0.048	0.033	0.031	0.032	0.025	0.034	34	1.08	1.00
58	3	0.045	0.033	0.032	0.035	0.023	0.034	35	0.95	0.93
44	2	0.045	0.033	0.033	0.030	0.024	0.033	36	0.97	0.98
996	SA	0.042	0.033	0.033	0.028	0.028	0.033	37	0.68	0.87
51	2	0.044	0.034	0.031	0.033	0.022	0.033	38	0.99	0.95
56	3	0.043	0.036	0.030	0.032	0.022	0.033	39	0.93	0.89
61	3	0.047	0.029	0.029	0.033	0.021	0.032	40	1.22	0.96
25	1	0.041	0.031	0.028	0.031	0.026	0.031	41	0.74*	0.93
36	2	0.043	0.030	0.030	0.027	0.021	0.030	42	0.99	0.98
46	2	0.044	0.030	0.029	0.027	0.021	0.030	43	1.09	0.99
59	3	0.041	0.027	0.031	0.028	0.021	0.030	44	0.92	0.94
35	2	0.037	0.028	0.035	0.022	0.025	0.029	45	0.59	0.50
52	2	0.039	0.024	0.028	0.022	0.022	0.027	46	0.86	0.88
Tmean#		0.048	0.035	0.034	0.033	0.027	0.035			

#Fmean and Tmean refer to the means of those families across all sites and the means of those tests across all families respectively.

*Regression coefficients (b₁) differs significantly from 1 (*P>0.1; **P>0.05; ***P>0.01)

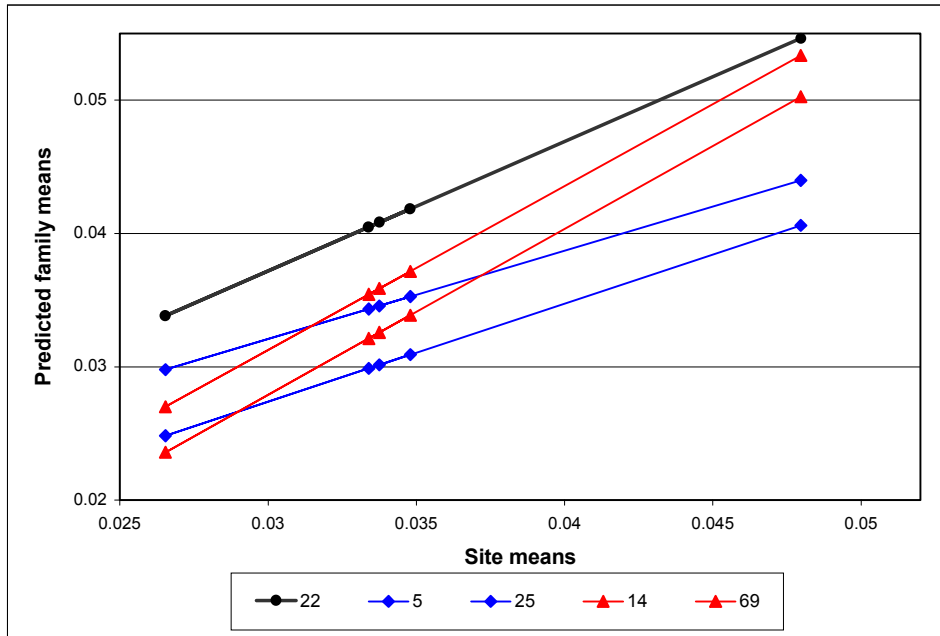


Figure 5.4.1: The predicted regression lines when plotting the predicted means of 5 treatments over the means for 5 sites at 5 years for CAMCORE series 01. Treatments selected includes a good performer with a regression coefficient around $b_1 = 1$, 2 stable performers with $b_1 < 1$, and 2 reactive treatments with $b_1 > 1$.

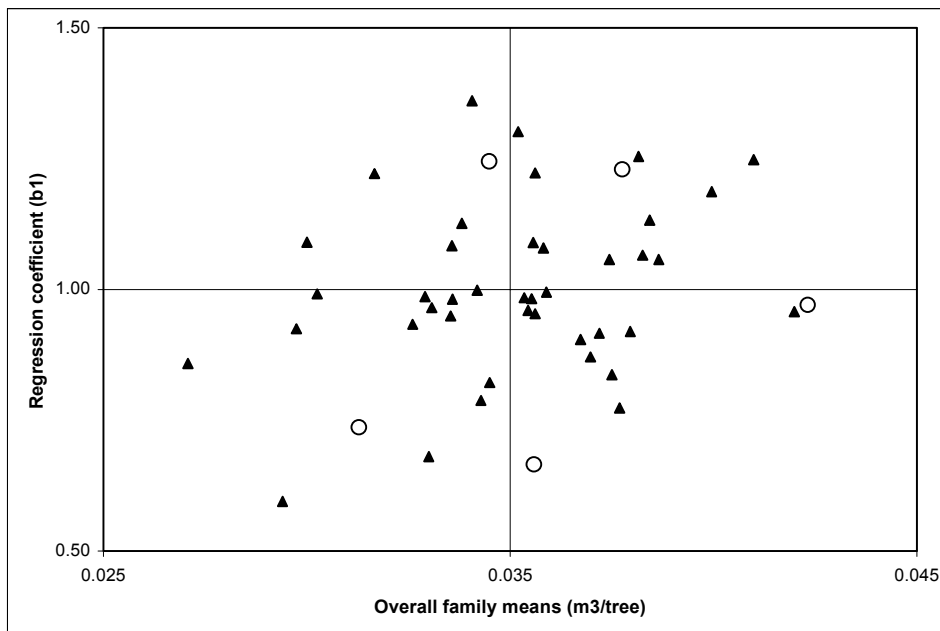


Figure 5.4.2: Fitted regression coefficients plotted against overall treatment means in volume per tree at 5 years for CAMCORE series 01. Treatments marked with a circle refer to those selected in figure 5.3.1.

5.4.2.3 Amongst the provenances in CAMCORE series 01, no significant differences in response were detected (Table 5.4.1). Looking at the individual treatments (Mexican OP families and genetic checks), only 4 treatments were identified as having a slope significantly different from 1 (Table 5.4.2). This represents 4/46 treatments or 9% of the genotypes. Amongst these interacting genotypes some rank changes are apparent (Figure 5.4.1). The distribution of genotypes appears to be scattered amongst those categorized as good & unstable (upper right quarter), good & stable (lower right quarter), poor & stable (lower left quarter) and poor & unstable (upper left quarter) (Figure 5.4.2).

5.4.2.4 Joint regression analysis using the CAMCORE 02/03 series

see tables 5.4.3 and 5.4.4 and figures 5.4.3 and 5.4.4.

Table 5.4.3: Volume / tree (V5) for each provenance at 5 years of age, at each of 6 sites in CAMCORE series 02 & 03, estimated regression coefficients (b_1) and the coefficient of determination (R^2) for regression models. Provenances included are (1) = Potrero de Monroy, (4) = El Manzanal, (5) = El Tlacuache, (6) = Ixtlan, (7) = Santa Maria Papalo and (SA) = South African genetic checks or controls.

Prov	20-07-02D	20-10-03A1	20-10-03A2	20-18-02E	20-10-02A	20-10-02B	Pmean	Rank	b_1	R^2
4	0.039	0.031	0.021	0.014	0.019	0.007	0.022	1	1.05	0.91
5	0.035	0.029	0.026	0.015	0.019	0.010	0.022	2	0.84	0.93
6	0.037	0.035	0.027	0.022	0.018	0.008	0.025	3	1.05	0.98
7	0.039	0.033	0.030	0.026	0.023	0.010	0.027	4	0.92	0.99
1	0.046	0.039	0.035	0.034	0.029	0.015	0.033	5	1.00	0.98
SA	0.048	0.041	0.038	0.037	0.028	0.015	0.034	6	1.08	0.95
Tmean#	0.041	0.035	0.030	0.025	0.023	0.011	0.027			

#Pmean and Tmean refer to the means of those provenances across all sites and the means of those tests across all provenances respectively.

Regression coefficients (b_1) differs significantly from 1 ($P>0.1$; ** $P>0.05$; *** $P>0.01$)

Table 5.4.4: Volume / tree (V5) for each common family / seedlot at 5 years of age, at each of 4 sites CAMCORE in series 02, estimated regression coefficients (b_1) and the coefficient of determination (R^2) for regression models. Provenances included are (1) = Potrero de Monroy, (4) = El Manzanal, (5) = El Tlacuache, (6) = Ixtlan, (7) = Santa Maria Papalo and (SA) = South African genetic checks or controls.

Fam	Prov	20-07-02D	20-18-02E	20-10-02A	20-10-02B	Fmean	Rank	b_1	R^2
999	SA	0.056	0.035	0.029	0.016	0.034	1	1.35**	1.00
997	SA	0.049	0.042	0.028	0.017	0.034	2	1.10	0.87
10	1	0.046	0.033	0.034	0.016	0.032	3	0.97	0.95
5	1	0.046	0.037	0.028	0.017	0.032	4	0.96	0.94
998	SA	0.047	0.035	0.026	0.013	0.030	5	1.16	0.95
996	SA	0.041	0.035	0.028	0.015	0.030	6	0.85	0.88
11	1	0.048	0.032	0.024	0.013	0.029	7	1.18	0.98
159	7	0.042	0.031	0.028	0.013	0.029	8	0.95	0.96
107	5	0.046	0.028	0.026	0.014	0.028	9	1.10*	1.00
168	7	0.045	0.029	0.025	0.011	0.027	10	1.14	0.99
150	6	0.051	0.026	0.021	0.009	0.027	11	1.43*	0.99
167	7	0.043	0.026	0.024	0.014	0.027	12	1.01	1.00
169	7	0.041	0.029	0.024	0.011	0.026	13	0.98	1.00
163	7	0.042	0.025	0.024	0.012	0.026	14	1.01	1.00

Table 5.4.4 continued...

Fam	Prov	20-07-02D	20-18-02E	20-10-02A	20-10-02B	Fmean	Rank	b ₁	R ²
170	7	0.040	*	0.024	0.012	0.026	15	0.93	0.97
160	7	0.042	0.027	0.023	0.010	0.025	16	1.05	0.99
172	7	0.040	0.027	0.023	0.011	0.025	17	0.98	0.99
154	6	0.040	0.027	0.022	0.011	0.025	18	0.97	0.99
161	7	0.034	0.024	0.026	0.011	0.024	19	0.73	0.93
141	6	0.040	0.024	0.023	0.008	0.024	20	1.05	0.99
148	6	0.045	0.023	0.016	0.010	0.023	21	1.20	0.95
166	7	0.035	0.027	0.022	0.009	0.023	22	0.85	0.91
171	7	0.038	0.027	0.020	0.008	0.023	23	0.98	0.96
95	4	0.038	0.012	0.019	*	0.023	24	1.25	0.85
100	4	0.036	0.014	0.019	*	0.023	25	1.10	0.91
145	6	0.041	0.022	0.017	0.009	0.022	26	1.08	0.97
138	6	0.039	0.023	0.019	0.007	0.022	27	1.09	1.00
177	7	0.033	0.025	0.021	0.008	0.022	28	0.81	0.95
78	4	0.043	0.015	0.022	0.007	0.022	29	1.19	0.90
87	4	0.036	0.013	0.021	0.017	0.022	30	0.64	0.61
98	4	0.038	0.018	0.022	0.008	0.022	31	0.99	0.95
125	5	0.031	0.014	0.019	*	0.021	32	0.83	0.88
174	7	0.033	0.023	0.018	0.011	0.021	33	0.75*	0.98
83	4	0.035	0.012	0.016	*	0.021	34	1.21	0.91
156	6	0.038	0.019	0.018	0.009	0.021	35	0.97	0.98
135	6	0.038	0.021	0.016	0.008	0.021	36	1.03	0.99
118	5	0.032	0.009	0.021	*	0.021	37	0.94	0.62
152	6	0.033	0.025	0.018	0.007	0.021	38	0.86	0.94
102	4	0.041	0.017	0.019	0.005	0.020	39	1.20	0.97
153	6	0.036	0.019	0.017	0.009	0.020	40	0.91	0.99
134	6	0.035	0.018	0.018	0.009	0.020	41	0.90	0.98
90	4	0.040	0.013	0.021	0.006	0.020	42	1.11	0.88
147	6	0.038	0.019	0.016	0.007	0.020	43	1.03	0.98
144	6	0.032	0.024	0.017	0.007	0.020	44	0.83	0.92
164	7	0.033	0.019	0.020	0.006	0.020	45	0.89	0.97
88	4	0.044	0.010	0.019	0.005	0.020	46	1.30	0.87
80	4	0.038	0.013	0.016	0.011	0.019	47	0.94	0.84
86	4	0.041	0.012	0.019	0.005	0.019	48	1.19	0.88
85	4	0.037	0.017	0.016	0.007	0.019	49	1.02	0.98
130	5	0.039	0.013	0.018	0.005	0.019	50	1.12	0.93
123	5	0.031	0.009	0.016	*	0.019	51	1.04	0.82
131	5	0.039	0.013	0.020	0.002	0.018	52	1.23	0.94
151	6	0.031	0.020	0.015	0.007	0.018	53	0.81*	0.99
128	5	0.038	0.009	0.017	0.002	0.017	56	1.19	0.88
124	5	0.034	0.012	0.018	0.001	0.016	57	1.09	0.94
119	5	0.033	0.009	0.017	0.003	0.015	58	0.98	0.89
149	6	0.027	0.014	0.012	0.006	0.015	59	0.72**	0.99
126	5	0.023	0.009	0.015	0.007	0.014	60	0.53	0.80
Tmean		0.041	0.025	0.023	0.011	0.025			

#Fmean and Tmean refer to the means of those families across all sites and the means of those tests across all families respectively.

*Regression coefficients (b₁) differs significantly from 1 (*P>0.1; **P>0.05; ***P>0.01)

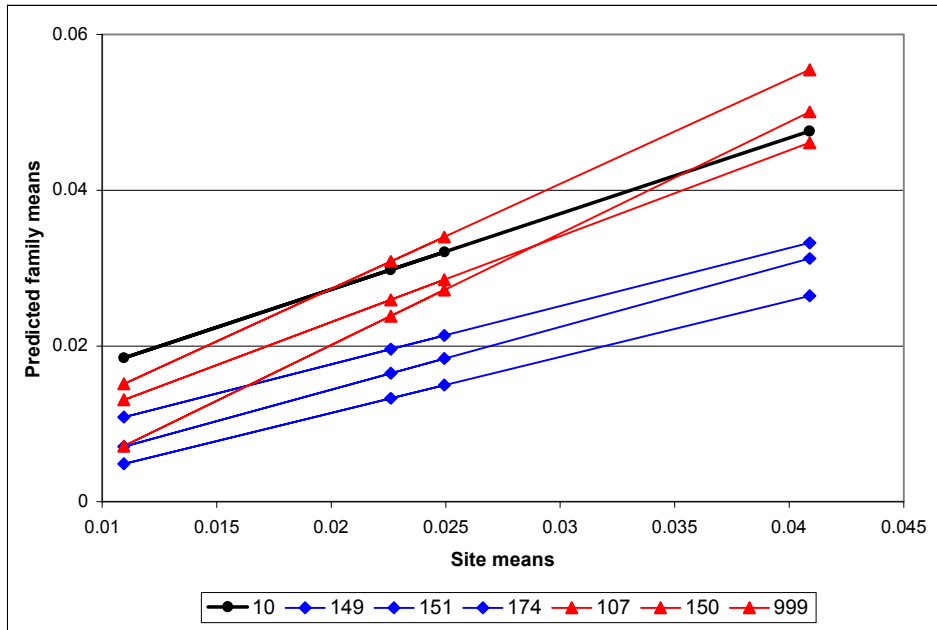


Figure 5.4.3: The predicted regression lines when plotting the predicted means of 7 treatments over the means for 4 sites at 5 years for CAMCORE series 02. Treatments selected includes a good performer with a regression coefficient around $b_1 = 1$, 3 stable performers with $b_1 < 1$, and 3 reactive treatments with $b_1 > 1$.

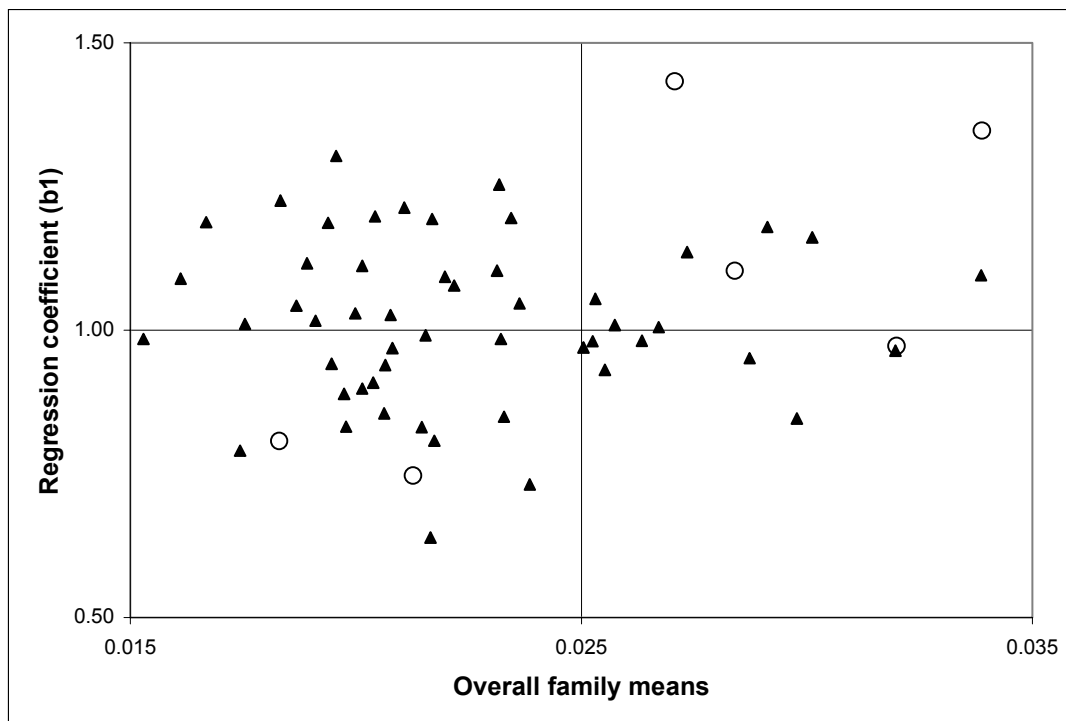


Figure 5.4.4: Fitted regression coefficients plotted against overall treatment means in volume per tree at 5 years for CAMCORE series 02. Treatments marked with a circle refer to those selected in figure 5.4.3.

5.4.2.5 Amongst the provenances in CAMCORE series 02 no significant differences in response was detected (Table 5.4.3). Looking at the individual treatments (Mexican OP families and genetic checks), only 6 treatments were identified as having a slope significantly different from 1 (Table 5.4.4). This represents 6/60 treatments or 10% of the genotypes. Amongst these interacting genotypes some rank changes are apparent (Figure 5.4.3). The distribution of genotypes appears to be scattered amongst those categorized as good & unstable (upper right quarter), good & stable (lower right quarter), poor & stable (lower left quarter) and poor & unstable (upper left quarter) (Figure 5.4.4).

5.4.2.6 Joint regression analysis using the CAMCORE 05 series

see table 5.4.5 and 5.4.6 and figures 5.4.5 to 5.4.8.

Table 5.4.5: Volume / tree (V5) for each provenance at 5 years of age, at each of 5 sites in CAMCORE series 05, estimated regression coefficients (b_1) and the coefficient of determination (R^2) for regression models. Provenances included are (1) = Potrero de Monroy, (8) = Conrado Castillo, (10) = Tlacotla, (11) = Pinal de Amoles, (12) = Zacualtipan, (13) = Llano de las Carmonas and (SA) = South African genetic checks or controls.

Prov	20-07-05L	20-10-05F	20-18-05K	20-10-05E1	20-10-05E2	Pmean#	Rank	b_1^*	R^2
SA	0.054	0.038	0.039	0.031	0.016	0.036	1	1.18	0.97
1	0.052	0.042	0.037	0.030	0.018	0.036	2	1.09	0.99
12	0.050	0.041	0.037	0.027	0.016	0.034	3	1.13*	0.99
11	0.044	0.037	0.036	0.023	0.017	0.032	4	0.95	0.98
13	0.046	0.036	0.033	0.025	0.017	0.031	5	0.96	0.99
8	0.041	0.035	0.032	0.025	0.017	0.030	6	0.82***	0.99
10	0.041	0.032	0.035	0.022	0.015	0.029	7	0.87	0.96
Tmean#	0.047	0.037	0.036	0.026	0.017	0.032			

#Pmean and Tmean refer to the means of those provenances across all sites and the means of those tests across all provenances respectively.

Regression coefficients (b_1) differs significantly from 1 ($P > 0.1$; ** $P > 0.05$; *** $P > 0.01$)

Table 5.4.6: Volume / tree (V5) for each common family / seedlot at 5 years of age, at each of 5 sites in CAMCORE series 05, estimated regression coefficients (b_1) and the coefficient of determination (R^2) for regression models. Provenances included are (1) = Potrero de Monroy, (8) = Conrado Castillo, (10) = Tlacotla, (11) = Pinal de Amoles, (12) = Zacualtipan, (13) = Llano de las Carmonas and (SA) = South African genetic checks or controls.

Fam	Prov	20-07-05L	20-10-05F	20-18-05K	20-10-05E1	20-10-05E2	Fmean	Rank	B_1^*	R^2
10	1	0.052	0.044	0.036	0.034	*	0.041	1	0.94	0.86
256	12	0.055	0.052	0.041	0.031	0.016	0.039	2	1.41*	0.96
999	SA	0.060	0.036	0.040	0.036	0.014	0.038	3	1.39	0.85
251	12	0.052	0.044	0.041	0.032	0.018	0.037	4	1.18	0.98
227	8	0.051	0.046	0.039	0.031	0.019	0.037	5	1.14	0.98
11	1	0.052	0.048	0.038	0.030	0.016	0.037	6	1.28	0.95
997	SA	0.056	*	0.040	0.035	0.016	0.037	7	1.33	0.96
258	12	0.056	0.043	0.038	0.028	0.017	0.036	8	1.34**	0.99
998	SA	0.053	0.039	0.044	0.028	0.018	0.036	9	1.24	0.97
214	11	0.048	0.040	0.044	0.028	0.019	0.036	10	1.08	0.94

Table 5.4.6 continued....

Fam	Prov	20-07-05L	20-10-05F	20-18-05K	20-10-05E1	20-10-05E2	Fmean	Rank	B ₁ *	R ²
225	8	0.051	0.043	0.039	0.027	0.020	0.036	11	1.12*	0.99
262	12	0.049	0.043	0.036	0.031	0.018	0.035	12	1.06	0.97
254	12	0.050	0.048	0.039	0.028	0.012	0.035	13	1.40	0.95
241	8	0.047	0.041	0.040	0.030	0.018	0.035	14	1.01	0.98
5	1	0.051	0.043	0.036	0.027	0.019	0.035	15	1.14	0.98
222	11	0.050	0.039	0.039	0.027	0.019	0.035	16	1.08	0.99
230	8	0.049	0.044	0.033	0.028	0.018	0.034	17	1.10	0.93
218	11	0.050	0.040	0.037	0.026	0.019	0.034	18	1.10	0.99
284	13	0.048	0.036	0.037	0.027	0.018	0.033	19	1.01	0.98
252	12	0.048	0.040	0.037	0.024	0.015	0.033	20	1.17**	1.00
208	11	0.048	0.038	0.036	0.023	0.017	0.032	21	1.11	0.99
202	11	0.048	0.034	0.036	0.027	0.016	0.032	22	1.04	0.97
211	11	0.050	0.039	0.034	0.022	0.016	0.032	23	1.21	0.98
228	8	0.037	0.045	0.031	0.031	0.017	0.032	24	0.78	0.68
212	11	0.043	0.037	0.038	0.022	0.019	0.032	25	0.93	0.94
280	13	0.048	0.036	0.032	0.027	0.017	0.032	26	1.04	0.97
286	13	0.048	0.043	0.032	0.022	0.015	0.032	27	1.23	0.96
272	13	0.050	0.036	0.030	0.026	0.017	0.032	28	1.07	0.92
243	8	0.043	0.034	0.037	0.027	0.018	0.032	29	0.87	0.97
264	13	0.044	0.034	0.033	0.028	0.019	0.031	30	0.82	0.96
265	13	0.043	0.038	*	0.026	0.018	0.031	31	0.92	0.99
217	11	0.042	0.037	0.036	0.025	0.017	0.031	32	0.91	0.98
219	11	0.048	0.038	0.036	0.018	0.015	0.031	33	1.24	0.95
199	11	0.045	0.041	0.033	0.019	0.016	0.031	34	1.13	0.93
295	10	0.042	0.034	0.038	0.023	0.017	0.031	35	0.92	0.93
233	8	0.040	0.038	0.035	0.024	0.017	0.031	36	0.89	0.95
996	SA	0.047	*	0.034	0.025	0.017	0.031	37	1.04	0.99
209	11	0.043	0.033	0.034	0.026	0.017	0.031	38	0.89	0.98
220	11	0.040	0.041	0.034	0.022	0.015	0.030	39	1.00	0.91
205	11	0.040	0.035	0.036	0.022	0.016	0.030	40	0.91	0.95
290	10	0.043	0.030	0.036	0.025	0.015	0.030	41	0.94	0.92
237	8	0.044	0.036	0.031	0.022	0.016	0.030	42	0.99	0.98
285	13	0.043	0.034	0.034	0.022	0.015	0.030	43	1.02	0.99
240	8	0.034	0.034	0.031	0.026	0.016	0.028	48	0.66*	0.91
231	8	0.039	0.030	0.030	0.024	0.016	0.028	49	0.77**	0.98
221	11	0.036	0.030	0.033	0.022	0.016	0.027	50	0.73*	0.95
245	8	0.036	0.029	0.030	0.025	0.014	0.027	51	0.74*	0.94
210	11	0.030	0.034	0.032	0.023	0.015	0.027	52	0.63	0.79
239	8	0.036	0.029	0.033	0.019	0.017	0.027	53	0.75	0.90
242	8	0.033	0.029	0.028	0.021	0.015	0.025	54	0.64***	0.99
289	10	0.037	0.027	0.029	0.020	0.011	0.025	55	0.90	0.98
232	8	0.038	0.026	0.024	0.021	0.014	0.025	56	0.76	0.91
234	8	0.030	0.026	0.027	0.017	0.015	0.023	57	0.58***	0.94
Tmean		0.047	0.037	0.036	0.026	0.017	0.032			

#Fmean and Tmean refer to the means of those families across all sites and the means of those tests across all families respectively.

*Regression coefficients (b₁) differs significantly from 1 (*P>0.1; **P>0.05; ***P>0.01)

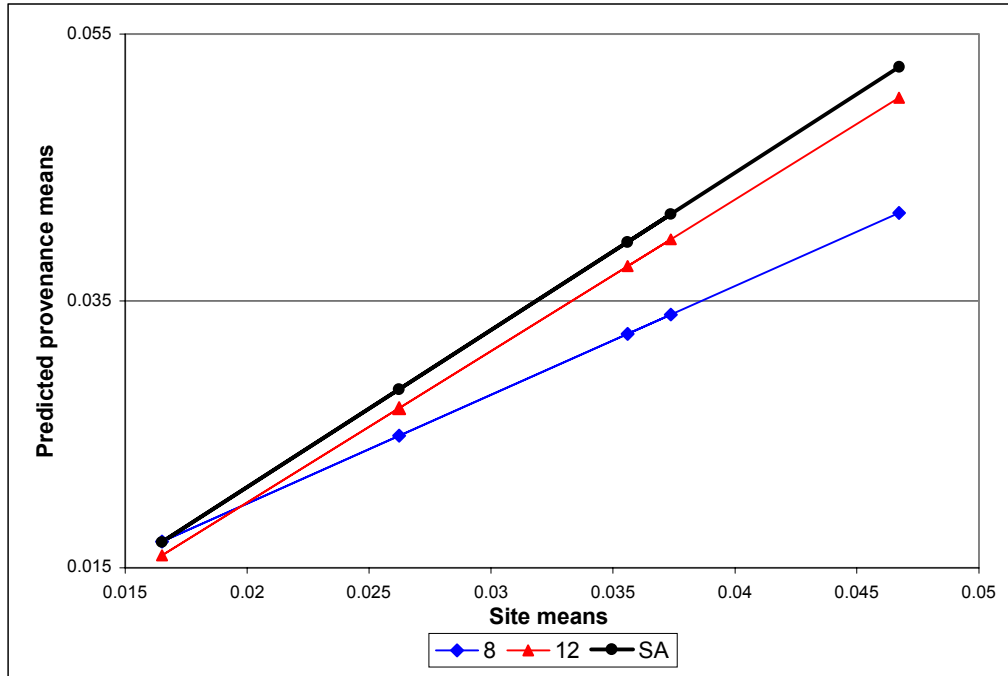


Figure 5.4.5: The predicted regression lines when plotting the predicted means of 3 provenances over the means for 5 sites at 5 years for CAMCORE series 05. Treatments selected includes the SA 'provenance', 1 stable performer with $b_1 < 1$, and 1 reactive treatments with $b_1 > 1$.

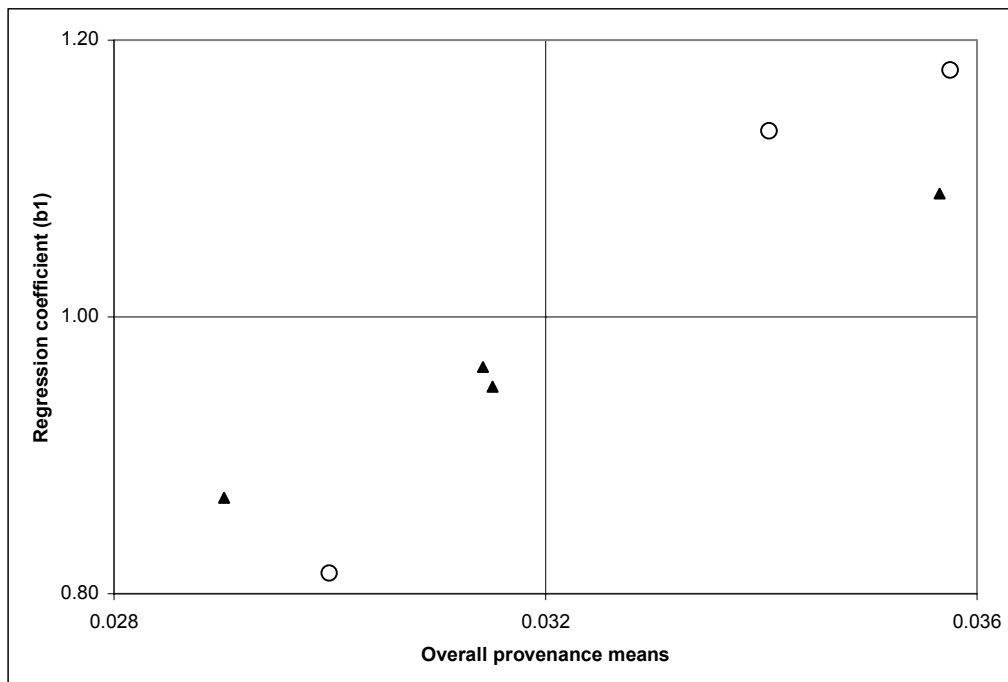


Figure 5.4.6: Fitted regression coefficients plotted against overall provenance means in volume per tree at 5 years for CAMCORE series 05. Treatments marked with a circle refer to those selected in figure 5.4.5.

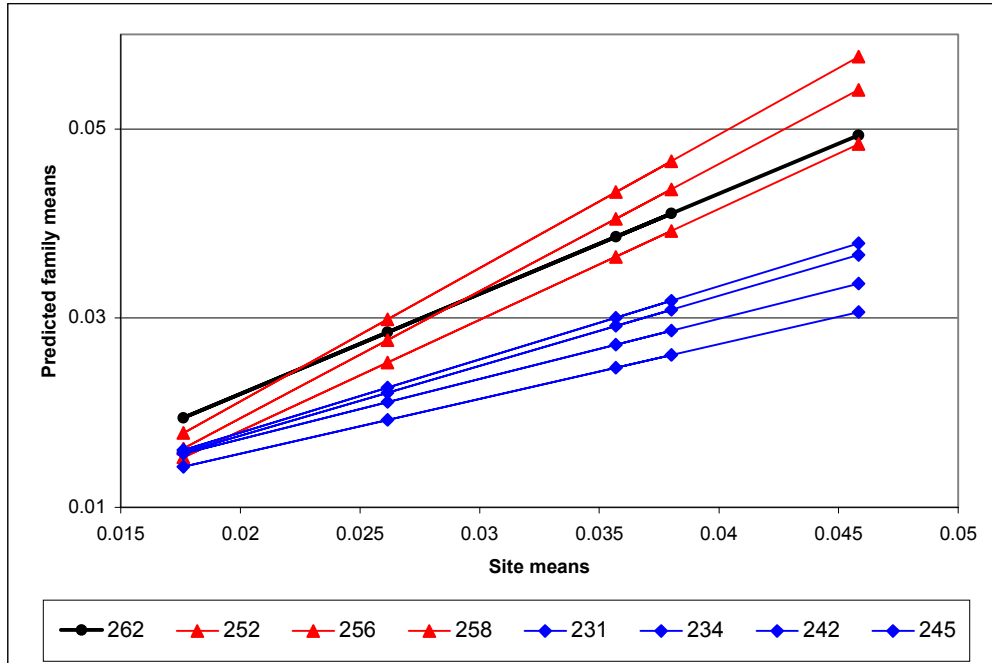


Figure 5.4.7: The predicted regression lines when plotting the predicted means of 8 treatments over the means for 5 sites at 5 years for CAMCORE series 05. Treatments selected includes a good performer with a regression coefficient around $b_1 = 1$, 3 stable performers with $b_1 < 1$, and 4 reactive treatments with $b_1 > 1$.

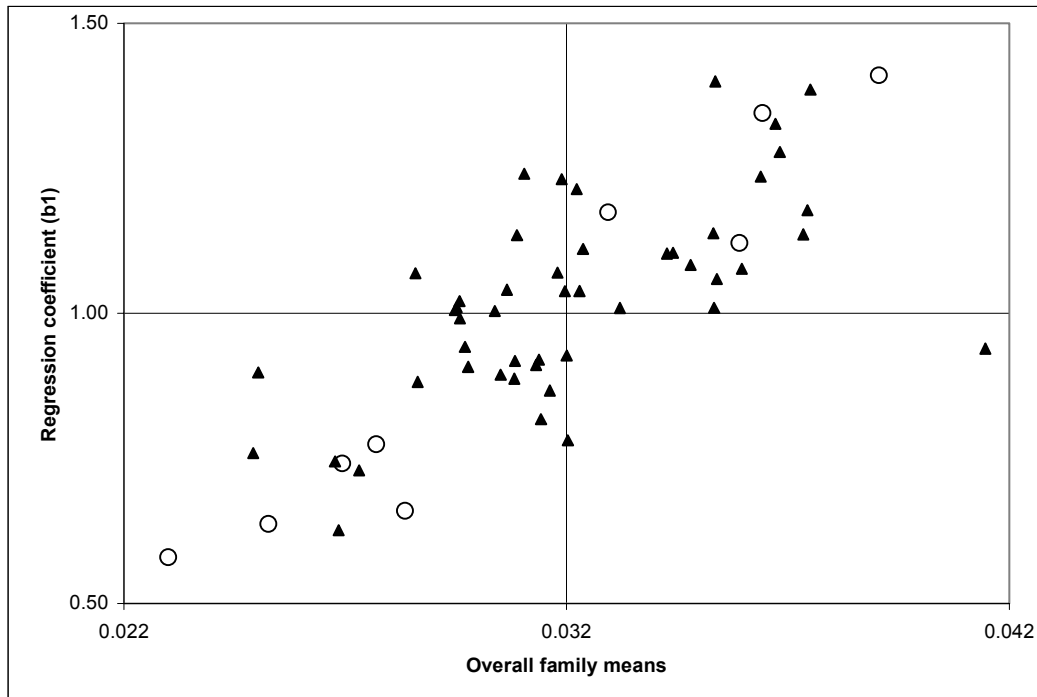


Figure 5.4.8: Fitted regression coefficients plotted against overall treatment means in volume per tree at 5 years for CAMCORE series 05. Treatments marked with a circle refer to those selected in figure 5.4.7.

5.4.2.7 Significant differences amongst the provenances for CAMCORE trial series 05 were detected (Table 5.4.5). Conrado Castillo was more stable and the Zacualtipan more unstable than the other provenances tested. Looking at the individual treatments (Mexican OP families and genetic checks), only 10 treatments were identified as having a slope significantly different from 1 (Table 5.4.6). This represents 10/57 treatments or 18% of the genotypes. Amongst the interacting provenances, the Conrado Castillo provenance appears to be relatively better on the poorer sites (Figure 5.4.5). Amongst the interacting genotypes, on a family level, some rank changes are apparent (Figure 5.4.7). The distribution of genotypes appears to be scattered primarily amongst those categorized as good & unstable (upper right quarter), and poor & stable (lower left quarter). There are relatively few genotypes in the lower right quarter (good & stable) and upper left quarter (poor & unstable) (Figure 5.4.8).

5.4.2.8 Joint regression analysis using the CAMCORE 06 series

see tables 5.4.7 and 5.4.8 and figures 5.4.9 – 5.4.12.

Table 5.4.7: Volume / tree (V5) for each provenance at 5 years of age, at each of 4 sites in CAMCORE series 06, estimated regression coefficients (b_1) and the coefficient of determination (R^2) for regression models. Provenances included are (1) = Potrero de Monroy, (8) = Conrado Castillo, (10) = Tlacotla, (11) = Pinal de Amoles, (13) = Llano de las Carmonas and (SA) = South African genetic checks or controls.

Prov	20-07-06E	20-18-06D	20-10-06B1	20-10-06B2	Pmean#	Rank	B_1^*	R^2
SA	0.065	0.038	0.020	0.018	0.035	1	1.22**	1.00
1	0.064	0.035	0.019	0.019	0.034	2	1.21***	1.00
11	0.054	0.034	0.022	0.021	0.033	3	0.88***	1.00
13	0.056	0.030	0.019	0.018	0.031	4	0.99	0.99
8	0.047	0.030	0.020	0.017	0.029	5	0.77**	0.99
10	0.051	0.030	0.015	0.018	0.029	6	0.92	0.99
Tmean#	0.056	0.033	0.019	0.019	0.032			

#Pmean and Tmean refer to the means of those provenances across all sites and the means of those tests across all provenances respectively.

Regression coefficients (b_1) differs significantly from 1 ($P > 0.1$; ** $P > 0.05$; *** $P > 0.01$)

Table 5.4.8: Volume / tree (V5) for each common family / seedlot at 5 years of age, at each of 4 sites in CAMCORE series 06, estimated regression coefficients (b_1) and the coefficient of determination (R^2) for regression models. Provenances included are (1) = Potrero de Monroy, (8) = Conrado Castillo, (10) = Tlacotla, (11) = Pinal de Amoles, (13) = Llano de las Carmonas and (SA) = South African genetic checks or controls.

Fam	Prov	20-07-06E	20-18-06D	20-10-06B1	20-10-06B2	Fmean	Rank	b_1	R^2
10	1	0.061	0.033	0.020	*	0.038	1	1.17	1.00
997	SA	0.072	0.041	0.019	0.019	0.038	2	1.51***	1.00
203	11	0.062	0.039	0.021	0.023	0.036	3	1.13	0.99
999	SA	0.065	0.036	0.024	0.019	0.036	4	1.25*	0.99
998	SA	0.065	0.040	0.020	0.018	0.036	5	1.31*	0.99
288	13	0.064	0.032	0.023	0.021	0.035	6	1.19	0.98
216	11	0.063	0.035	0.020	0.022	0.035	7	1.19**	1.00
207	11	0.054	0.039	0.023	0.023	0.035	8	0.88	0.98
11	1	0.067	0.040	0.020	0.012	0.035	9	1.46	0.97
215	11	0.053	0.037	0.026	0.023	0.035	10	0.82*	0.99
268	13	0.071	0.029	0.020	0.018	0.035	11	1.47	0.97
5	1	0.063	0.033	0.016	0.022	0.034	12	1.24	0.98
287	13	0.055	0.034	0.021	0.020	0.033	13	0.96*	1.00
996	SA	0.058	0.035	0.019	0.018	0.032	14	1.12*	1.00
206	11	0.054	0.032	0.023	0.019	0.032	15	0.95	0.99
226	8	0.050	0.034	0.024	0.019	0.032	16	0.80	0.97
213	11	0.052	0.031	0.021	0.020	0.031	17	0.91**	1.00
305	10	0.056	*	0.020	0.017	0.031	18	1.08	1.00
263	13	0.055	0.027	0.018	0.020	0.030	19	1.00	0.98
278	13	0.052	0.030	0.020	0.018	0.030	20	0.93	1.00
229	8	0.050	0.029	0.020	0.018	0.029	21	0.88	0.99
276	13	0.051	0.030	0.017	0.018	0.029	22	0.96	1.00
271	13	0.051	0.030	0.017	0.018	0.029	23	0.95*	1.00
248	12	0.050	0.028	0.018	0.018	0.029	24	0.90*	1.00
247	8	0.046	0.031	0.020	0.017	0.029	25	0.79	0.98
301	10	0.051	0.029	0.015	0.019	0.029	26	0.97	0.98
224	8	0.044	0.030	0.021	0.018	0.028	27	0.69**	0.98
246	8	0.046	0.030	0.019	0.016	0.028	28	0.80	0.98
277	13	0.049	0.028	0.019	0.015	0.028	29	0.91	0.99
292	10	0.051	0.027	0.014	0.018	0.028	30	0.99	0.98
236	8	0.045	*	0.019	0.017	0.027	31	0.75*	1.00
201	11	0.041	0.025	0.018	0.018	0.025	32	0.66***	0.99
244	8	0.043	0.024	0.018	0.016	0.025	33	0.75*	0.98
235	8	*	0.031	0.019	0.018	0.023	34	1.00	1.00
283	13	*	0.028	0.017	0.014	0.020	35	0.98	0.95
Tmean		0.055	0.033	0.020	0.020	0.032			

#Fmean and Tmean refer to the means of those families across all sites and the means of those tests across all families respectively.

Regression coefficients (b_1) differs significantly from 1 ($P > 0.1$; ** $P > 0.05$; *** $P > 0.01$)

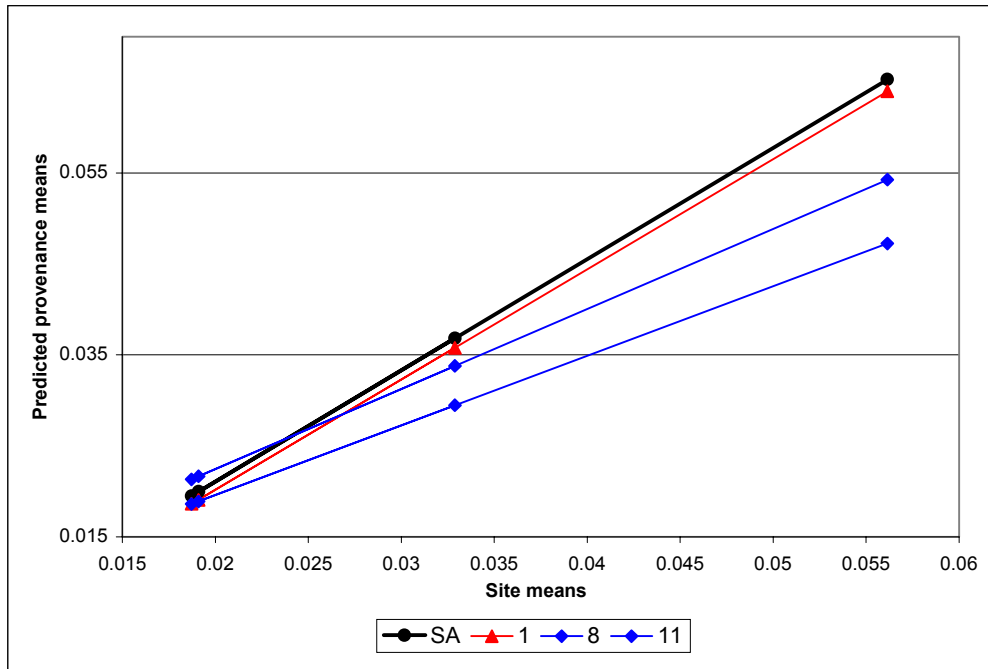


Figure 5.4.9: The predicted regression lines when plotting the predicted means of 4 provenances over the means for 4 sites at 5 years for CAMCORE series 06. Treatments selected includes the SA 'provenance', 2 stable performers with $b_1 < 1$, and 1 reactive treatments with $b_1 > 1$.

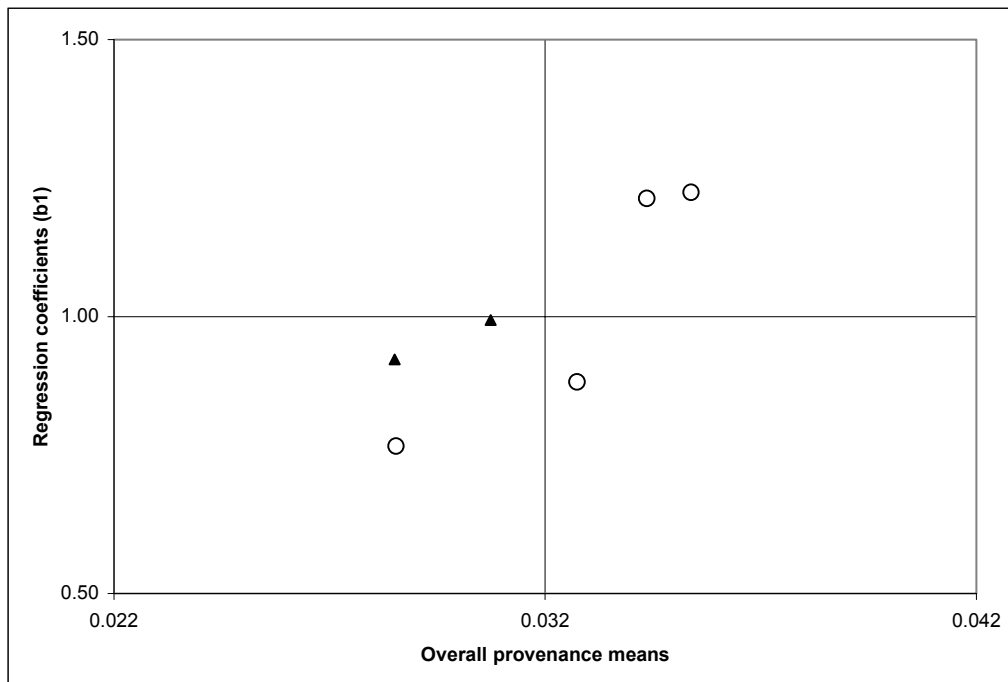


Figure 5.4.10: Fitted regression coefficients plotted against overall provenance means in volume per tree at 5 years for CAMCORE series 06. Treatments marked with a circle refer to those selected in figure 5.4.9.

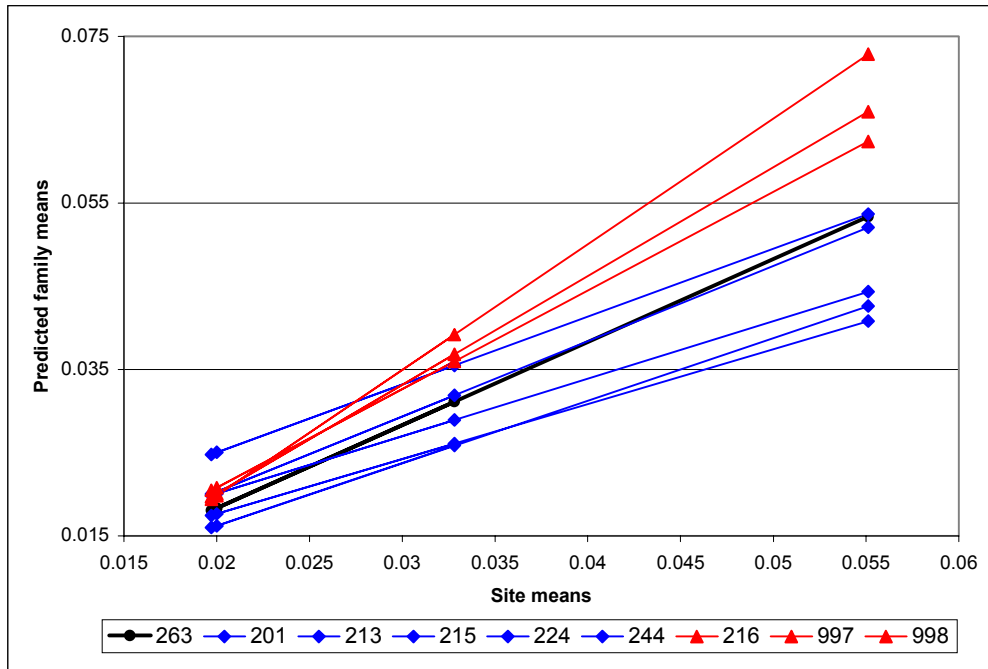


Figure 5.4.11: The predicted regression lines when plotting the predicted means of 9 treatments over the means for 4 sites at 5 years for CAMCORE series 06. Treatments selected include a good performer with a regression coefficient around $b_1 = 1$, 5 stable performers with $b_1 < 1$, and 3 reactive treatments with $b_1 > 1$.

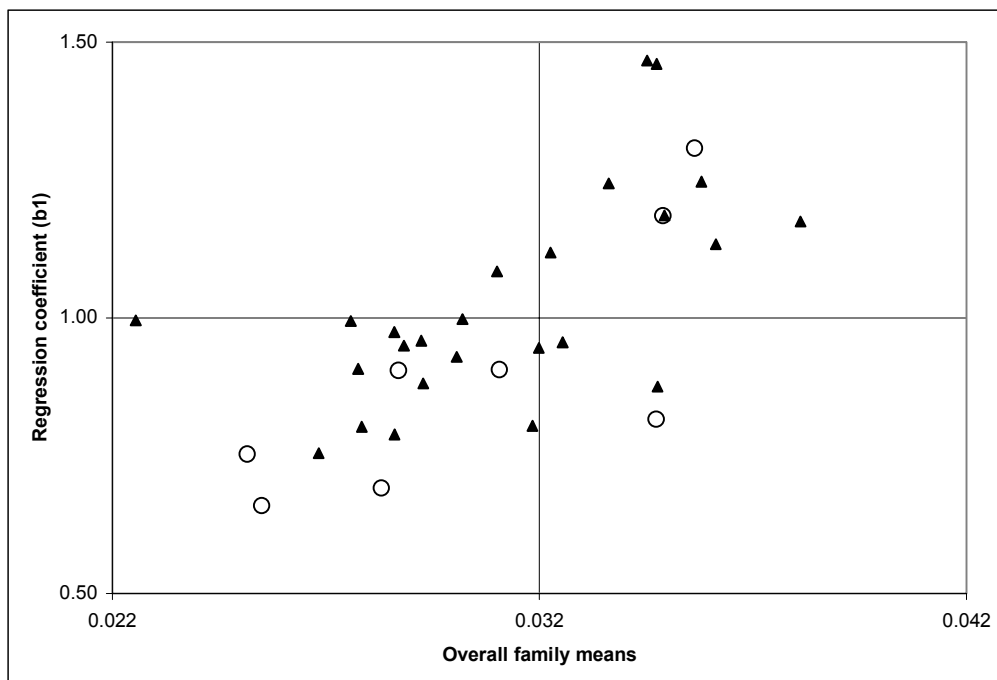


Figure 5.4.12: Fitted regression coefficients plotted against overall treatment means in volume per tree at 5 years for CAMCORE series 06. Treatments marked with a circle refer to those selected in figure 5.4.11.

5.4.2.9 Significant differences amongst the provenances for CAMCORE trial series 06 were detected (Table 5.4.7). The provenances of Conrado Castillo and Pinal de Amoles were more stable, and Potrero de Monroy and the South African genetic checks more responsive to an increase in site quality. Looking at the individual treatments (Mexican OP families and genetic checks), 14 treatments were identified as having a slope significantly different from 1 (Table 5.4.8). This represents 14/35 treatments or 40% of the genotypes. Amongst the interacting provenances, Pinal de Amoles and, to a lesser extent Conrado Castillo provenance appear to be relatively better on the poorer sites (Figure 5.4.9). Amongst the interacting genotypes, on a family level, some rank changes are apparent (Figure 5.4.11). The distribution of genotypes appears to be scattered primarily amongst those categorized as good & unstable (upper right quarter), and poor & stable (lower left quarter). There are relatively few genotypes in the lower right quarter (good & stable) and upper left quarter (poor & unstable) (Figure 5.4.12).

5.4.2.10 Joint regression analysis using the CAMCORE 07 series

see tables 5.4.9 and 5.4.10 and figures 5.4.13 – 5.4.16.

Table 5.4.9: Volume / tree (V5) for each provenance at 5 years of age, at each of 4 sites in CAMCORE series 07, estimated regression coefficients (b_1) and the coefficient of determination (R^2) for regression models. Provenances included are (8) = Conrado Castillo, (11) = Pinal de Amoles, (13) = Llano de las Carmonas and (SA) = South African genetic checks or controls.

Prov	20-07-07D	20-18-07A	20-10-07B1	20-10-07B2	Pmean#	Rank	B_1^*	R^2
SA	0.060	0.035	0.031	0.018	0.036	1	1.19**	1.00
11	0.052	0.032	0.028	0.018	0.033	2	0.98	1.00
13	0.052	0.030	0.023	0.018	0.031	3	1.04	0.99
8	0.045	0.030	0.026	0.018	0.030	4	0.79**	1.00
Tmean#	0.053	0.032	0.027	0.018	0.032			

#Pmean and Tmean refer to the means of those provenances across all sites and the means of those tests across all provenances respectively.

Regression coefficients (b_1) differs significantly from 1 ($P > 0.1$; ** $P > 0.05$; *** $P > 0.01$)

Table 5.4.10: Volume / tree (V5) for each common family / seedlot at 5 years of age, at each of 4 sites in CAMCORE series 07, estimated regression coefficients (b_1) and the coefficient of determination (R^2) for regression models. Provenances included are (8) = Conrado Castillo, (11) = Pinal de Amoles, (13) = Llano de las Carmonas and (SA) = South African genetic checks or controls.

Fam	Prov	20-07-07D	20-18-07A	20-10-07B1	20-10-07B2	Fmean#	Rank	b_1^*	R^2
11	1	0.061	0.039	0.032	*	0.044	1	1.06	1.00
5	1	0.057	0.039	0.031	*	0.042	2	0.96	0.99
10	1	0.057	0.037	0.031	*	0.042	3	0.96**	1.00
999	SA	0.063	0.034	0.037	0.019	0.038	4	1.20	0.94
998	SA	0.062	0.035	0.031	0.021	0.037	5	1.17	0.99
997	SA	0.064	0.034	0.033	0.017	0.037	6	1.30	0.98
200	11	0.057	0.036	0.031	0.022	0.036	7	1.01	1.00
223	8	0.048	0.033	0.025	*	0.035	8	0.82	0.98
203	11	0.058	0.035	0.028	0.019	0.035	9	1.11***	1.00
305	10	0.057	0.039	0.028	0.015	0.035	10	1.17	0.97
249	12	0.059	0.032	0.030	0.019	0.035	11	1.12	0.99
207	11	0.055	0.031	0.034	0.019	0.035	12	0.96	0.93
281	13	0.050	0.033	0.022	*	0.035	13	1.01	0.97
215	11	0.052	0.033	0.032	0.021	0.034	14	0.85	0.98
263	13	0.059	0.032	0.025	0.018	0.034	15	1.20*	0.99
269	13	0.059	0.032	0.023	0.021	0.033	16	1.17	0.96
287	13	0.054	0.033	0.027	0.019	0.033	17	1.00	1.00
271	13	0.045	0.032	0.020	*	0.032	18	0.85	0.92
300	10	0.052	0.034	0.024	0.016	0.032	19	1.02	0.98
996	SA	0.051	0.036	0.023	0.016	0.032	20	1.03	0.96
226	8	0.045	0.034	0.028	0.018	0.031	21	0.74	0.96
229	8	0.046	0.031	0.026	0.017	0.030	22	0.81*	0.99
206	11	0.051	0.028	0.026	0.014	0.030	23	1.02	0.99
273	13	0.048	*	0.024	0.017	0.030	24	0.89*	1.00
248	12	0.046	0.030	0.027	0.015	0.029	25	0.83	0.97
246	8	0.043	0.028	0.025	0.019	0.029	26	0.70***	1.00
276	13	0.050	0.027	0.023	0.013	0.028	27	1.03	1.00
275	13	0.054	0.024	0.018	0.016	0.028	28	1.16	0.95
224	8	0.044	0.026	0.025	0.016	0.028	29	0.79*	0.99
201	11	0.043	0.026	0.021	0.016	0.027	30	0.80**	1.00
Tmean#		0.053	0.033	0.027	0.018	0.033			

#Fmean and Tmean refer to the means of those families across all sites and the means of those tests across all families respectively.

Regression coefficients (b_1) differs significantly from 1 ($P > 0.1$; ** $P > 0.05$; *** $P > 0.01$)

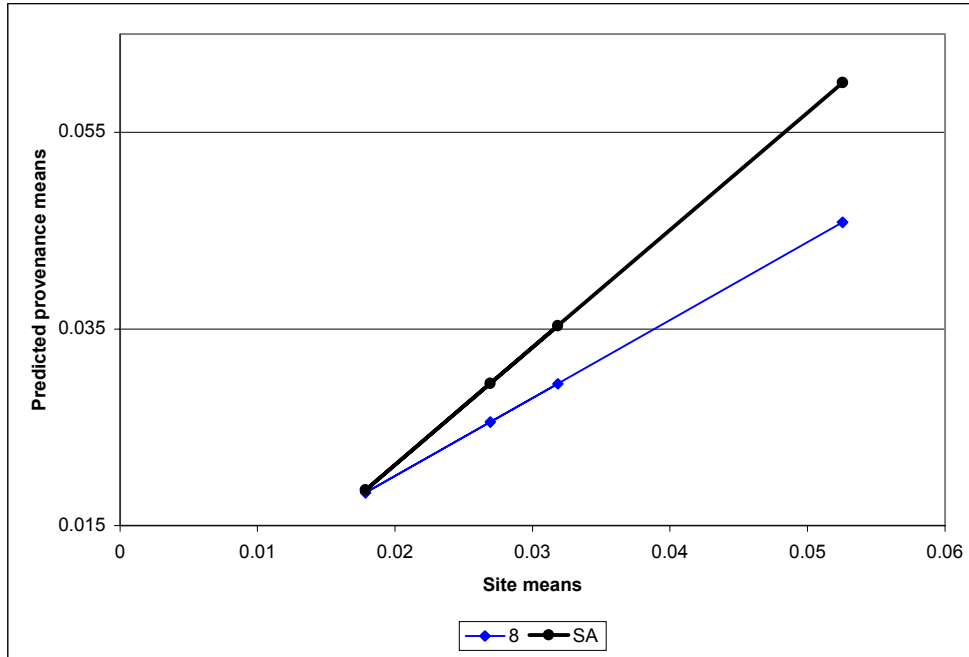


Figure 5.4.13: The predicted regression lines when plotting the predicted means of 2 provenances over the means for 4 sites at 5 years for CAMCORE series 07. Treatments selected includes the SA 'provenance' and 1 stable performers with $b_1 < 1$.

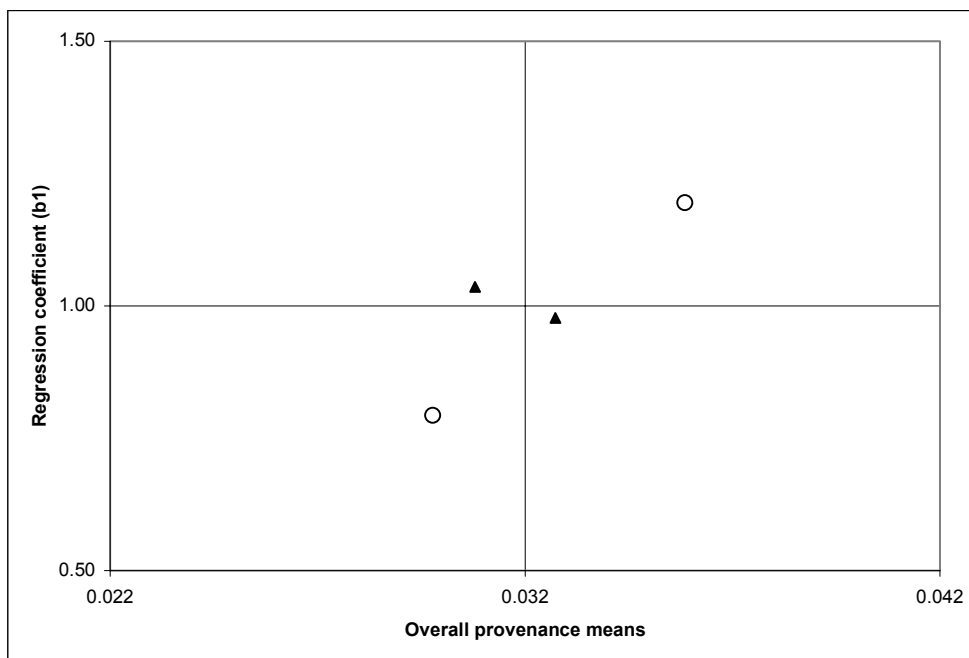


Figure 5.4.14: Fitted regression coefficients plotted against overall provenance means in volume per tree at 5 years for CAMCORE series 07. Treatments marked with a circle refer to those selected in figure 5.4.13.

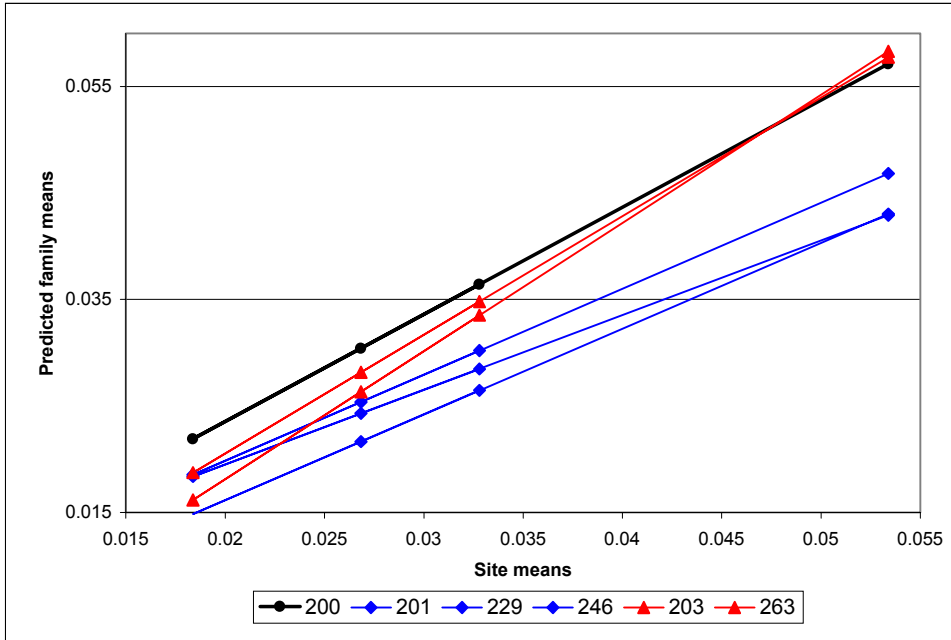


Figure 5.4.15: The predicted regression lines when plotting the predicted means of 6 treatments over the means for 4 sites at 5 years for CAMCORE series 07. Treatments selected includes a good performer with a regression coefficient around $b_1 = 1$, 3 stable performers with $b_1 < 1$, and 2 reactive treatments with $b_1 > 1$.

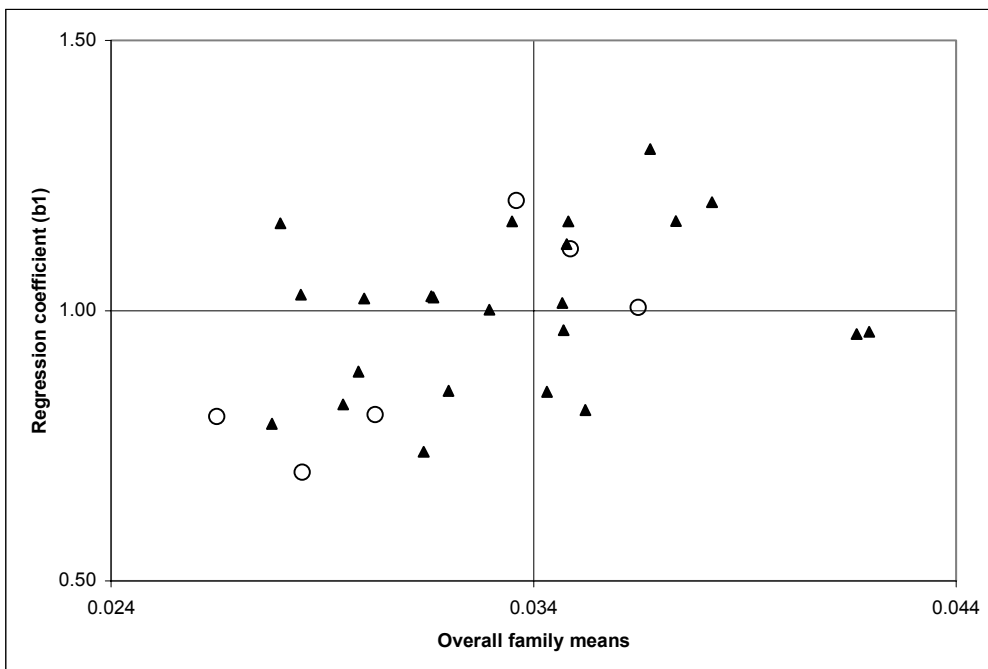


Figure 5.4.16: Fitted regression coefficients plotted against overall treatment means in volume per tree at 5 years for CAMCORE series 07. Treatments marked with a circle refer to those selected in figure 5.4.15.

5.4.2.11 Significant differences amongst the provenances for CAMCORE trial series 07 were detected (Table 5.4.9). Conrado Castillo was more stable and the South African genetic checks more responsive to an increase in site quality. Looking at the individual treatments (Mexican OP families and genetic checks), 8 treatments were identified as having a slope significantly different from 1 (Table 5.4.10). This represents 8/30 treatments or 27% of the genotypes. Amongst the interacting provenances, Conrado Castillo appears to perform relatively better on the poorer sites (Figure 5.4.13). Amongst the interacting genotypes, on a family level, some rank changes are apparent (Figure 5.4.15). The distribution of genotypes appears to be scattered amongst those categorised as good & unstable (upper right quarter), good & stable (lower right quarter), poor & stable (lower left quarter) and poor & unstable (upper left quarter) (Figure 5.4.16); although there are relatively few genotypes in the lower right quarter (good & stable quarter).

5.4.2.12 Joint regression analysis using the ICFR series

see table 5.4.11 and figures 5.4.17 and 5.4.18.

Table 5.4.11: Volume / tree (V6) for each common family / seedlot at 6 years of age, at each of 5 sites in the ICFR series, estimated regression coefficients (b_1) and the coefficient of determination (R^2) for regression models.

Fam	Graskop	Bulwer	Helvetia	Usutu	Ugie	Fmean#	Rank	b_1^*	R^2
165	0.082	0.063	0.069	0.054	0.039	0.061	1	1.34	0.95
170	0.087	0.068	0.054	0.050	0.035	0.059	2	1.60	0.92
4000	0.083	0.056	0.060	0.061	0.032	0.059	3	1.40	0.82
184	0.079	0.058	0.055	0.056	0.040	0.058	4	1.07	0.85
171	0.076	0.067	0.055	0.057	0.033	0.058	5	1.31	0.92
149	0.065	0.069	0.059	0.049	0.041	0.057	6	0.91	0.84
3000	0.080	0.056	0.053	0.062	0.030	0.056	7	1.36	0.77
61	0.069	0.065	0.061	0.051	0.034	0.056	8	1.17	0.97
189	0.065	0.058	0.064	0.052	0.041	0.056	9	0.79	0.87
74	0.069	0.067	0.056	0.049	0.039	0.056	10	1.01	0.93

Table 5.4.11 continued...

Fam	Graskop	Bulwer	Helvetia	Usutu	Ugie	Fmean#	Rank	b ₁ *	R ²
231	0.076	0.061	0.061	0.047	0.033	0.056	11	1.35***	0.99
160	0.067	0.063	0.062	0.041	0.039	0.054	12	1.04	0.84
13	0.073	0.057	0.050	0.054	0.036	0.054	13	1.04	0.85
248	0.064	0.056	0.060	0.044	0.043	0.053	14	0.74	0.83
168	0.066	0.057	0.053	0.053	0.035	0.053	15	0.93	0.93
75	0.062	0.064	0.055	0.041	0.039	0.052	16	0.88	0.80
183	0.063	0.062	0.058	0.044	0.034	0.052	17	1.03	0.92
169	0.067	0.056	0.059	0.044	0.034	0.052	18	1.09	0.96
9	0.060	0.064	0.055	0.046	0.036	0.052	19	0.86	0.85
177	0.065	0.056	0.058	0.044	0.038	0.052	20	0.90	0.95
229	0.067	0.060	0.055	0.045	0.033	0.052	21	1.09	0.99
193	0.068	0.057	0.052	0.048	0.034	0.052	22	1.05	0.98
91	0.069	0.051	0.055	0.045	0.037	0.051	23	0.96	0.91
42	0.063	0.061	0.053	0.045	0.031	0.051	24	1.07	0.95
4	0.063	0.055	0.055	0.051	0.027	0.050	25	1.12	0.92
52	0.060	0.060	0.054	0.043	0.033	0.050	26	0.95	0.93
200	0.060	0.053	0.051	0.046	0.039	0.050	27	0.67***	1.00
48	0.062	0.052	0.058	0.045	0.030	0.050	28	1.04	0.92
15	0.067	0.060	0.047	0.044	0.030	0.050	29	1.20	0.94
146	0.061	0.051	0.058	0.042	0.032	0.049	30	0.97	0.90
87	0.062	0.053	0.050	0.045	0.034	0.049	31	0.86**	0.99
219	0.053	0.055	0.055	0.045	0.034	0.049	32	0.68	0.79
6	0.063	0.054	0.046	0.051	0.029	0.049	33	0.98	0.85
244	0.063	0.056	0.054	0.036	0.032	0.048	34	1.08	0.91
153	0.065	0.050	0.055	0.043	0.026	0.048	35	1.20	0.95
10	0.059	0.053	0.053	0.040	0.032	0.047	36	0.91	0.96
55	0.065	0.050	0.049	0.043	0.030	0.047	37	1.05	0.97
69	0.065	0.049	0.047	0.041	0.033	0.047	38	0.97	0.92
22	0.063	0.052	0.046	0.043	0.032	0.047	39	0.94	0.96
72	0.061	0.052	0.046	0.040	0.034	0.047	40	0.88	0.94
28	0.058	0.052	0.047	0.042	0.034	0.046	41	0.78**	0.98
6000	0.055	0.056	0.047	0.042	0.031	0.046	42	0.83	0.90
67	0.055	0.053	0.051	0.043	0.029	0.046	43	0.88	0.93
266	0.056	0.051	0.048	0.041	0.031	0.045	44	0.83***	1.00
58	0.054	0.051	0.049	0.039	0.034	0.045	45	0.71*	0.94
224	0.055	0.046	0.052	0.042	0.029	0.045	46	0.82	0.90
78	0.057	0.052	0.044	0.035	0.030	0.044	47	0.91	0.93
47	0.058	0.038	0.046	0.044	0.029	0.043	48	0.77	0.74
Tmean#	0.065	0.056	0.054	0.046	0.034	0.051			

#Fmean and Tmean refer to the means of those families across all sites and the means of those tests across all families respectively.

*Regression coefficients (b₁) differs significantly from 1 (*P>0.1; **P>0.05; ***P>0.01)

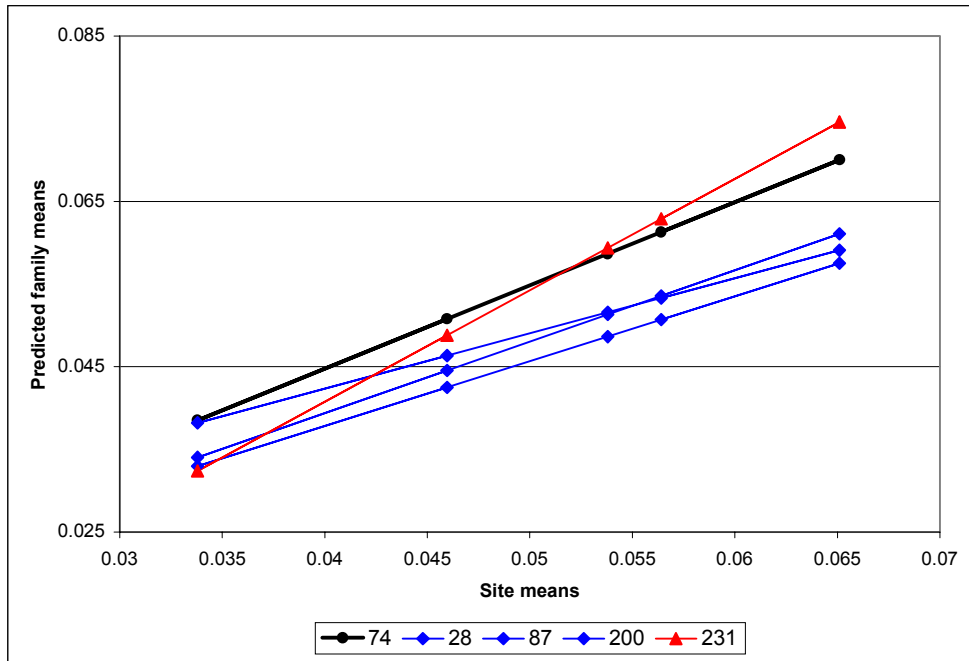


Figure 5.4.17: The predicted regression lines when plotting the predicted means of 5 treatments over the means for 5 sites at 6 years for ICFR series. Treatments selected includes a good performer with a regression coefficient around $b_1 = 1$, 3 stable performers with $b_1 < 1$, and 1 reactive treatments with $b_1 > 1$.

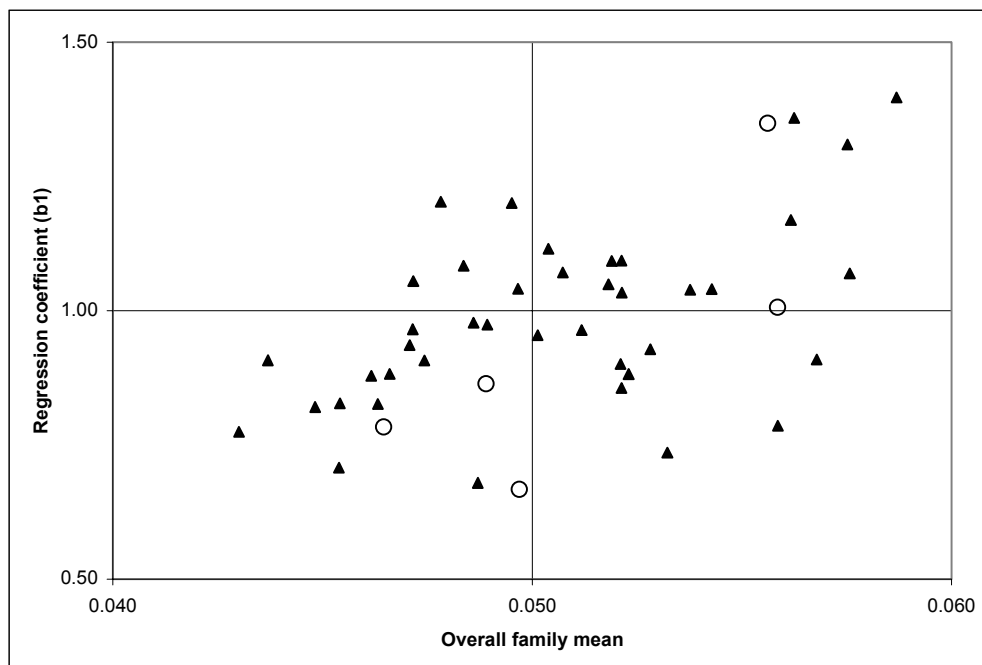


Figure 5.4.18: Fitted regression coefficients plotted against overall treatment means in volume per tree at 6 years for ICFR series. Treatments marked with a circle refer to those selected in figure 5.4.17.

5.4.2.13 Significant differences in response amongst the ICFR series were detected. Amongst the individual treatments (1st generation OP families and genetic checks), 5 treatments were identified as having a slope significantly different from 1 (Table 5.4.11). This represents 5/48 treatments or 10% of the genotypes. Some rank changes are apparent (Figure 5.4.17). The distribution of genotypes appears to be scattered amongst those categorized as good & unstable (upper right quarter), good & stable (lower right quarter), poor & stable (lower left quarter) and poor & unstable (upper left quarter) (Figure 5.4.18).

5.4.2.14 Joint regression analysis using the Sappi series

see tables 5.4.12 and 5.4.13 and figures 5.4.19 – 5.4.22.

Table 5.4.12: Volume / tree (V5) for each common family / seedlot at 5 years of age, at each of 4 sites in the Sappi S1 series, estimated regression coefficients (b_1) and the coefficient of determination (R^2) for regression models.**

Trt	PG30	PG28	PG31	PG29	Fmean#	Rank	b_1^*	R^2
SB6	0.049	0.051	0.033	0.020	0.038	1	1.10	0.88
SB1	0.060	0.045	0.029	0.016	0.038	2	1.52***	1.00
MB3	0.059	0.041	0.028	0.018	0.036	3	1.39*	0.98
SB3	0.050	0.043	0.029	0.021	0.036	4	1.05	1.00
FB9	0.053	0.042	0.027	0.022	0.036	5	1.15	0.99
PB86	0.055	0.045	0.023	0.019	0.036	6	1.36	0.98
SB4	0.048	0.038	0.029	0.025	0.035	7	0.80	0.97
FB2	0.048	0.044	0.029	0.019	0.035	8	1.08	0.97
MB6	0.054	0.042	0.026	0.019	0.035	9	1.27**	1.00
FB5	0.055	0.038	0.027	0.019	0.035	10	1.23	0.97
ZA5	0.048	0.039	0.028	0.022	0.034	11	0.92*	1.00
PB122	0.049	0.041	0.024	0.023	0.034	12	1.00	0.95
cam5	0.047	0.039	0.027	0.021	0.034	13	0.92***	1.00
PB19	0.052	0.040	0.022	0.020	0.033	14	1.20	0.97
PB88	0.050	0.042	0.025	0.017	0.033	15	1.23**	1.00
PB114	0.045	0.043	0.025	0.020	0.033	16	1.00	0.96
ZA4	0.047	0.039	0.026	0.021	0.033	17	0.94	0.99
PB85	0.047	0.038	0.027	0.021	0.033	18	0.93*	1.00
SB2	0.047	0.036	0.028	0.021	0.033	19	0.89	0.98
PB116	0.044	0.040	0.028	0.020	0.033	20	0.87	0.98
FB8	0.044	0.037	0.028	0.022	0.033	21	0.78***	1.00
PB118	0.043	0.045	0.027	0.017	0.033	22	0.99	0.87
SB5	0.046	0.040	0.027	0.018	0.033	23	1.02	0.99
PB93	0.046	0.040	0.028	0.017	0.033	24	1.03	0.97
PB106	0.050	0.035	0.029	0.017	0.033	25	1.09	0.95
PB96	0.043	0.039	0.026	0.023	0.033	26	0.76	0.96
cam21	0.042	0.039	0.028	0.021	0.033	27	0.80	0.97
FB7	0.044	0.035	0.026	0.024	0.033	28	0.72	0.96
ZA1	0.046	0.039	0.026	0.019	0.032	29	1.00	1.00
MB2	0.050	0.037	0.025	0.018	0.032	30	1.11	0.99
cam22	0.048	0.043	0.021	0.018	0.032	31	1.22	0.95

Table 5.4.12 continued....

Trt	PG30	PG28	PG31	PG29	Fmean#	Rank	b ₁ *	R ²
PB101	0.048	0.038	0.025	0.018	0.032	32	1.07	1.00
MB5	0.047	0.035	0.026	0.020	0.032	33	0.95	0.98
PB107	0.047	0.038	0.026	0.017	0.032	34	1.07	1.00
PB40	0.039	0.041	0.029	0.019	0.032	35	0.73	0.83
PB100	0.042	0.039	0.024	0.021	0.032	36	0.83	0.96
MB1	0.045	0.038	0.026	0.017	0.032	37	1.01	0.99
PB90	0.046	0.036	0.023	0.021	0.032	38	0.91	0.97
PB119	0.048	0.037	0.025	0.017	0.032	39	1.10	1.00
cam11	0.048	0.035	0.024	0.019	0.032	40	1.02	0.97
FB1	0.046	0.037	0.023	0.019	0.031	41	1.00	0.99
PB97	0.047	0.037	0.024	0.016	0.031	42	1.10*	1.00
FB3	0.046	0.032	0.027	0.019	0.031	43	0.86	0.93
SAPMIX	0.046	0.036	0.021	0.021	0.031	44	0.95	0.94
MB4	0.047	0.036	0.022	0.019	0.031	45	1.04	0.98
Monmix2	0.054	0.034	0.019	0.016	0.031	46	1.36	0.93
PB112	0.045	0.043	0.024	0.011	0.031	47	1.27	0.93
PB115	0.039	0.040	0.026	0.018	0.031	48	0.82	0.90
FB6	0.043	0.037	0.024	0.018	0.031	49	0.90	0.99
FB4	0.043	0.035	0.024	0.019	0.030	50	0.89**	1.00
ZIMX	0.044	0.037	0.024	0.016	0.030	51	0.99	1.00
PB87	0.048	0.034	0.024	0.015	0.030	52	1.12	0.98
PB89	0.048	0.032	0.025	0.015	0.030	53	1.10	0.95
ZA6	0.043	0.037	0.022	0.015	0.029	54	1.01	0.98
ZA3	0.043	0.035	0.025	0.014	0.029	55	1.00	0.99
P10011	0.040	0.030	0.028	0.017	0.029	56	0.70	0.89
cam12	0.041	0.030	0.025	0.018	0.029	57	0.74	0.95
PB120	0.039	0.034	0.026	0.014	0.028	58	0.85	0.92
ZA2	0.043	0.030	0.025	0.016	0.028	59	0.90	0.95
FB10	0.046	0.030	0.022	0.013	0.028	60	1.09	0.96
PB95	0.041	0.029	0.023	0.018	0.028	61	0.79	0.96
P10021	0.037	0.034	0.024	0.015	0.028	62	0.80	0.96
PB108	0.034	0.032	0.024	0.015	0.026	63	0.66	0.92
Tmean#	0.046	0.038	0.026	0.019	0.032			

#Fmean and Tmean refer to the means of those families across all sites and the means of those tests across all families respectively.

*Regression coefficients (b₁) differs significantly from 1 (*P>0.1; **P>0.05; ***P>0.01)

**S1 refers to the above 4 tests planted in 1996 and assessed at 5 years

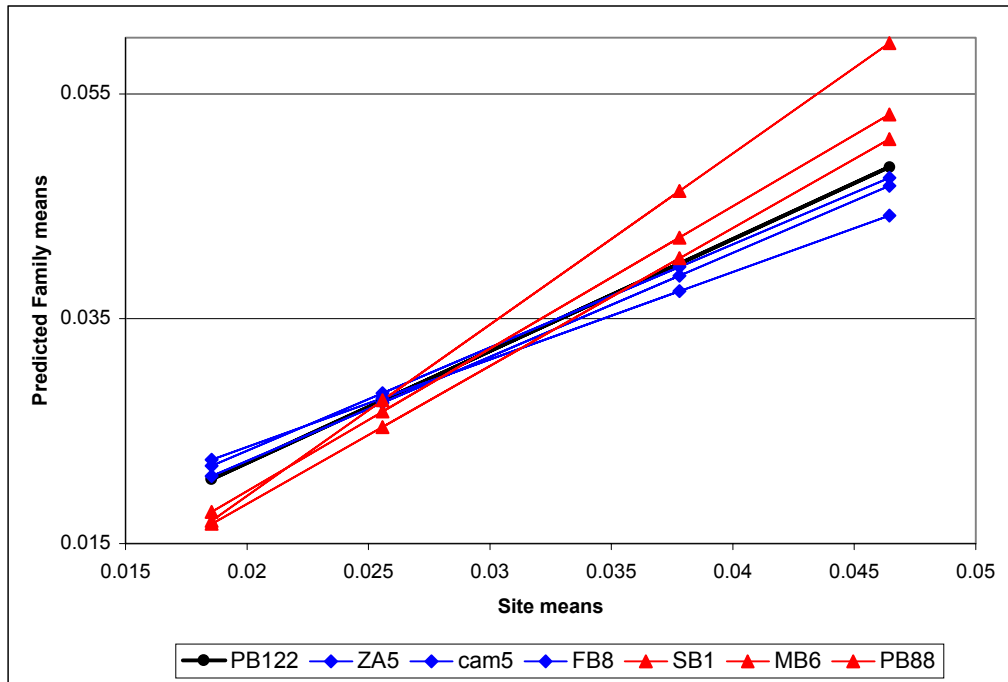


Figure 5.4.19: The predicted regression lines when plotting the predicted means of 7 treatments over the means for 4 sites at 5 years for Sappi S1 series. Treatments selected includes a good performer with a regression coefficient around $b_1 = 1$, 3 stable performers with $b_1 < 1$, and 3 reactive treatments with $b_1 > 1$.

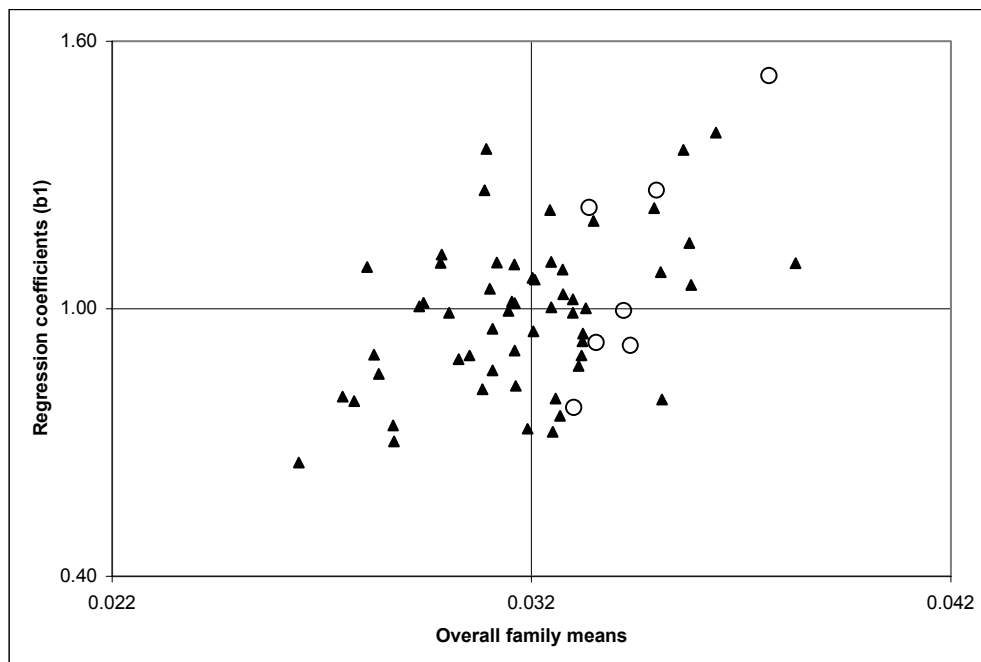


Figure 5.4.20: Fitted regression coefficients plotted against overall treatment means in volume per tree at 5 years for Sappi S1 series. Treatments marked with a circle refer to those selected in figure 5.4.19.

Table 5.4.13: Volume / tree (V4) for each common family / seedlot at 4 years of age, at each of 4 sites in the Sappi S2 series, estimated regression coefficients (b_1) and the coefficient of determination (R^2) for regression models.**

Trt	PG35	PG33	PG36	PG34	Fmean#	Rank	b_1^*	R^2
PB102	0.012	0.012	0.008	0.006	0.010	1	1.33	0.90
PB86	0.011	0.012	0.006	0.008	0.010	2	1.07	0.74
PB96	0.012	0.010	0.009	0.006	0.009	3	0.97	0.80
SAPMIX	0.011	0.012	0.006	0.008	0.009	4	0.97	0.72
PB90	0.011	0.012	0.006	0.006	0.009	5	1.38	0.91
PB112	0.013	0.010	0.005	0.006	0.008	6	1.59	0.96
PB110	0.011	0.010	0.007	0.006	0.008	7	1.05	0.96
PB92	0.011	0.010	0.005	0.007	0.008	8	1.29	0.92
PB118	0.011	0.009	0.005	0.007	0.008	9	1.04	0.84
ZA5	0.011	0.010	0.006	0.006	0.008	10	1.21	0.94
PB85	0.011	0.008	0.006	0.007	0.008	11	0.84	0.79
PB89	0.013	0.007	0.006	0.006	0.008	12	1.23	0.75
PB94	0.011	0.009	0.007	0.006	0.008	13	0.96	0.95
PB119	0.011	0.008	0.007	0.006	0.008	14	1.04	0.92
PB114	0.011	0.009	0.006	0.006	0.008	15	1.13	0.97
PB113	0.011	0.010	0.007	0.005	0.008	16	1.22	0.91
PB106	0.010	0.009	0.007	0.006	0.008	17	0.74	0.95
ZA3	0.010	0.010	0.006	0.005	0.008	18	1.13	0.95
Monmix2	0.011	0.008	0.006	0.007	0.008	19	0.98	0.86
ZIMX	0.010	0.008	0.007	0.006	0.008	20	0.74	0.93
ZA2	0.010	0.009	0.006	0.006	0.008	21	0.96	1.00
ZA4	0.012	0.008	0.005	0.006	0.008	22	1.23	0.90
PB19	0.010	0.008	0.006	0.007	0.008	23	0.77	0.88
PB88	0.010	0.008	0.006	0.005	0.008	24	1.03	0.96
PB109	0.009	0.010	0.007	0.005	0.008	25	0.88	0.83
PB101	0.010	0.009	0.006	0.006	0.008	26	0.90	0.97
ZA1	0.009	0.009	0.007	0.006	0.008	27	0.59	0.87
PB104	0.010	0.009	0.005	0.006	0.008	28	0.90	0.92
PB84	0.010	0.007	0.005	0.007	0.007	29	0.84	0.81
PB116	0.009	0.008	0.006	0.006	0.007	30	0.78*	0.98
PB107	0.009	0.009	0.007	0.005	0.007	31	0.71	0.87
PB115	0.009	0.009	0.006	0.005	0.007	32	1.04	0.91
ZA6	0.010	0.009	0.005	0.005	0.007	33	1.16*	1.00
PB93	0.009	0.009	0.005	0.005	0.007	34	0.92	0.97
PB122	0.011	0.007	0.006	0.005	0.007	35	1.12	0.82
PB120	0.009	0.007	0.006	0.006	0.007	36	0.65	0.90
PB108	0.010	0.009	0.004	0.005	0.007	37	1.26	0.95
PB105	0.009	0.009	0.006	0.005	0.007	38	0.81	0.94
PB99	0.009	0.009	0.006	0.004	0.007	39	0.90	0.83
PB95	0.009	0.007	0.007	0.005	0.007	40	0.60	0.75
PB117	0.010	0.007	0.005	0.005	0.007	41	0.99	0.84
PB97	0.010	0.008	0.005	0.005	0.007	42	1.08	0.98
PB8	0.009	0.006	0.005	0.006	0.007	43	0.72	0.75
PB91	0.010	0.007	0.005	0.004	0.007	44	1.21	0.92

Table 5.4.13 continued.....

Trt	PG35	PG33	PG36	PG34	Fmean#	Rank	b ₁ *	R ²
PB87	0.008	0.008	0.004	0.005	0.006	45	0.85	0.92
PB111	0.008	0.008	0.004	0.002	0.005	46	1.19	0.87
Tmean#	0.010	0.009	0.006	0.006	0.008			

#Fmean and Tmean refer to the means of those families across all sites and the means of those tests across all families respectively.

*Regression coefficients (b₁) differs significantly from 1 (*P>0.1; **P>0.05; ***P>0.01)

**S2 refers to the above 4 tests planted in 1997 and assessed at 4 years

5.4.2.15 Significant differences in response amongst both Sappi S1 & S2 trial series were detected (Table 5.4.12 & 5.4.13). Amongst the individual treatments in S1 (a range of 1st and 2nd generation OP families and genetic checks), 10 treatments were identified as having a slope significantly different from 1 (Table 5.4.12). This represents 10/63 treatments or 16% of the genotypes. For the S2 the figures are 2/46 or 4% (Table 5.4.13). Some rank changes are apparent in series 1 (Figure 5.4.19). The distribution of genotypes for this series appears to be scattered amongst those categorized as good & unstable (upper right quarter), good & stable (lower right quarter), poor & stable (lower left quarter) and poor & unstable (upper left quarter) (Figure 5.4.20).

5.4.3 Discussion

5.4.3.1 The proportion of genotypes that have a significantly different response from the remaining genotypes differs amongst the populations and sites sampled. Amongst the Mexican (CAMCORE) populations the proportion varies from 9 to 40%. The provenances sampled from the central area of the distribution of *P. patula* in Mexico (series 01) are at the one extreme with few reactive genotypes (9%). The proportion is much higher (18 – 40%) amongst the populations represented by both central and more northern provenances (series 05 – 07). Finally, the southern provenances (representing *P. patula* var. *longipedunculata*) had around 10% of families with responses that differed from the others.

5.4.3.2 When considering the provenances as a whole generally the more northern provenances were more interactive. In particular, Conrado Castillo and Pinal de Amoles tended to be more stable with regression coefficients less than 1. Potrero de Monroy and Zacualtipan on the other hand, representing the more central provenances, tended to be more reactive to site quality with regression coefficients greater than 1 at least when compared to the former populations. It is important to keep in mind that identifying genotypes (families or provenances) that respond in an average or interactive manner really only applies in the context of the populations and sites in which they are tested. A provenance such as Potrero de Monroy, or indeed the South African 'provenance' may be reactive to site (b₁ > 1) when tested with the northern populations (series 05

– 07) and average when tested with other central provenances (series 01). In other words the response is relative to the other material in the test.

5.4.3.3 It is also interesting to note that the South African genetic checks appear unstable when compared to the CAMCORE material in many tests. Generally they can be regarded as more reactive to site quality. This observation applies in particular to the improved material. These seedlots respond to better site quality which may simply indicate that the differences are not as marked on the poorer quality sites or that South African organizations are selecting genotypes that respond to site quality. Both of these are likely to contribute to this effect. The interpretation of this may have important implications. Have we identified amongst the CAMCORE material, provenances that do better than the South African material on the poorer sites or is it simply related to scale?

5.4.3.4 Amongst the South African progeny tests the proportion of reactive genotypes ranged from 4 – 16%. Within the 1st generation ICFR families the proportion was 10% and for the mainly 2nd generation Sappi S1 tests the proportion was around 16%. In contrast, only 4% of families in the Sappi S2 trials were interactive. This low proportion in the latter trial series may be attributable to the fact that, in essence, the 4 tests were only tested in 2 environments and, in addition, the precision in at least one of the tests (PG34) was quite low with a heritability of 0.07.

5.4.3.5 On the whole, the results from the analyses from the Type B genetic correlation estimates seem to relate well to the results from the joint regression technique. In both cases the techniques have identified the fact that more GxE was present amongst the northern provenances when compared to the central material. For the CAMCORE 01 – 04 series (southern and central provenances), the average Type B genetic correlation estimates were higher than for the CAMCORE 05 – 07 series. This corresponds to much lower numbers of interactive families being identified amongst the latter tests. In addition, even amongst the northern material the lowest Type B genetic correlations were estimated for the series 06 and this was also the series with the most interactive genotypes (Tables 5.4.7 and 5.4.8 and Figures 5.4.9 – 5.4.12).

5.4.3.6 In all of the above regressions genotypic response was plotted against the growth of all the genotypes on each site. In theory this should give a good indication of the productivity of the sites so that genotypic response could be related to site quality. This measure of 'site quality' could potentially be flawed because different organizations assessed these tests and, although these growth measurements should give us a good indication of relative performance between genotypes, it may be biased when comparing relative growth across sites. In other words the

environmental index used in the regressions may be biased. In addition, other environmental variables may be far more important in determining genotypic response and this will be considered further in later chapters.

5.5 An examination of actual rank changes

5.5.1 Introduction

5.5.1.1 The previous section identified some genotypes that differ in response to the environment and allowed some quantification of the relative proportion of these genotypes to the total. However it does not immediately follow that all of these entries differ significantly in terms of rank changes nor that they would necessarily have a dramatic impact on the selection of the best performing genotypes. A simple assessment of the actual performance and ranking of the genotypes in each environment should always be carried out in any GxE study to get a clearer picture of the extent of the rank changes and differences in response (Shelbourne, 1972).

5.5.2 Ranking of entry means and correlations between pairs of environments

5.5.2.1 For each of the selected trial series the treatments were ranked according to performance as estimated by the least square means in the GLM procedure in SAS. Treatment means were estimated for each site and for an overall estimate across all sites. In addition, Pearson correlation coefficients were calculated using the CORR procedure in SAS. The data is presented in the following tables.

5.5.2.2 CAMCORE series 01

Amongst those families that differ in their response to site quality there does appear to be some rank changes (Table 5.5.1). As examples, family 14 is ranked 4th in 20-07-01L and 19th in 20-10-01B and family 5 10th 20-18-01J and 37th in 20-07-01L. An examination of the phenotypic correlations indicates that simple phenotypic correlations also vary from 0.69 between 20-10-01B and 20-18-01H to 0.30 between 20-18-01J and 20-10-01A (Table 5.5.2). The former pair of sites are in relatively close proximity in one region whereas the latter 2 are further apart and differ considerably in a number of climatic characteristics. The average correlation for all pairs of sites is 0.52.

Table 5.5.1: The ranking of all common treatments for each individual test and the mean for all 5 tests as well as the regression coefficient (b_1), as calculated in the previous section, for the CAMCORE 01 series*. Provenances included are (1) = Potrero de Monroy, (2) = Ingenio del Rosario, (3) = Corralitla and (SA) = South African genetic checks or controls.

Prov	20-07-01L	20-10-01B	20-18-01J	20-10-01A	20-18-01H	Fmean	Rank	b_1
1	2	54	38	54	22	22	1	0.97
1	21	999	22	21	2	54	2	0.96
1	22	22	74	38	10	21	3	1.25
1	14	10	997	22	12	2	4	1.19
SA	997	21	27	57	27	16	5	1.06
3	54	7	16	55	21	74	6	1.13
1	26	57	6	997	7	57	7	1.07
1	16	67	7	41	6	997	8	1.25
3	57	74	10	67	54	10	9	0.92
3	74	27	5	2	9	14	10	1.23
3	73	62	67	74	999	27	11	0.77
2	45	16	45	16	16	38	12	0.84
1	9	11	54	999	57	67	13	1.06
1	12	8	35	73	5	7	14	0.92
1	10	2	14	62	11	999	15	0.87
1	8	26	2	14	996	6	16	0.90
3	69	997	50	48	14	12	17	0.99
3	67	56	21	58	8	9	18	1.08
1	7	14	8	71	66	45	19	1.22
1	6	9	66	64	50	5	20	0.66
1	11	6	11	12	38	50	21	0.95
3	66	66	69	50	74	8	22	1.09
SA	999	5	9	51	41	41	23	0.98
3	64	50	55	26	26	11	24	0.96
2	41	69	41	27	25	66	25	0.98
1	27	45	996	5	67	26	26	1.30
2	53	51	44	61	45	69	27	1.24
2	50	41	71	56	997	62	28	0.82
3	61	53	48	53	62	55	29	0.79
2	38	58	58	45	35	48	30	1.00
2	48	48	12	25	48	73	31	1.36
3	71	44	73	6	53	64	32	1.13
2	44	38	59	66	44	71	33	0.98
3	58	996	53	69	64	53	34	1.08
2	51	55	64	44	58	58	35	0.95
2	46	64	51	10	71	44	36	0.97
1	5	71	62	7	69	996	37	0.68
3	62	12	999	11	55	51	38	0.99
3	56	25	36	59	51	56	39	0.93
2	36	73	57	996	56	61	40	1.22
SA	996	36	56	8	73	25	41	0.74

Table 5.5.1 continued...

Prov	20-07-01L	20-10-01B	20-18-01J	20-10-01A	20-18-01H	Fmean	Rank	b ₁
3	55	46	46	9	52	36	42	0.99
3	59	61	61	36	36	46	43	1.09
1	25	35	26	46	59	59	44	0.92
2	52	59	52	52	46	35	45	0.59
2	35	52	25	35	61	52	46	0.86

*Shaded cells refer to regression coefficients significantly different from 1.

Table 5.5.2: Pearson correlation coefficients for all 5 tests for all common treatments in CAMCORE 01 series.

A.	20-07-01L	20-10-01B	20-18-01J	20-10-01A	20-18-01H	Mean
20-07-01L	1.00	0.65	0.43	0.55	0.62	0.56
p-value		<.0001	0.0032	<.0001	<.0001	
20-10-01B	0.65	1.00	0.51	0.55	0.69	0.60
p-value	<.0001		0.0003	<.0001	<.0001	
20-18-01J	0.43	0.51	1.00	0.30	0.59	0.46
p-value	0.0032	0.0003		0.043	<.0001	
20-10-01A	0.55	0.55	0.30	1.00	0.32	0.43
p-value	<.0001	<.0001	0.043		0.031	
20-18-01H	0.62	0.69	0.59	0.32	1.00	0.55
p-value	<.0001	<.0001	<.0001	0.031		
Mean	0.56	0.60	0.46	0.43	0.55	0.52

5.5.2.3 CAMCORE series 02

Amongst those treatments that differ in their response to site quality there does not appear to be many dramatic rank changes (Table 5.5.3). As examples the South African 2nd generation seed orchard seedlot (999) is ranked in the top 5 in all 4 tests and, similarly family 107 is ranked in the top 10 throughout. An examination of the correlation coefficients indicates that simple phenotypic correlations also vary relatively less, ranging from 0.75 between 20-10-02B and 20-18-02E to 0.51 between 20-10-02B and 20-07-02D (Table 5.5.4). The average correlation coefficient for all pairs of sites is 0.66.

Table 5.5.3: The ranking of all common treatments for each individual test and the mean for all 4 tests as well as the regression coefficient (b₁), as calculated in the previous section, for the CAMCORE 02 series*. Provenances included are (1) = Potrero de Monroy, (4) = El Manzanal, (5) = El Tlacuache, (6) = Ixtlan, (7) = Santa Maria Papalo and (SA) = South African genetic checks or controls.

Prov	20-07-02D	20-18-02E	20-10-02A	20-10-02B	Fmean	Rank	b ₁
SA	999	997	10	87	999	1	1.35
6	150	5	999	5	997	2	1.10
SA	997	996	5	997	10	3	0.97
1	11	998	996	10	5	4	0.96
SA	998	999	159	999	998	5	1.16

Table 5.5.3 continued....

Prov	20-07-02D	20-18-02E	20-10-02A	20-10-02B	Fmean	Rank	b ₁
5	107	10	997	996	996	6	0.85
1	10	11	107	167	11	7	1.18
1	5	159	998	107	159	8	0.95
7	168	168	161	159	107	9	1.10
6	148	107	168	11	168	10	1.14
4	88	166	163	998	150	11	1.43
7	167	171	11	163	167	12	1.01
4	78	160	167	161	163	13	1.01
7	159	172	141	154	160	14	1.05
7	163	154	172	172	172	15	0.98
7	160	150	160	174	154	16	0.97
4	86	167	166	168	161	17	0.73
4	102	177	78	80	141	18	1.05
6	145	152	154	148	148	19	1.20
SA	996	163	98	160	166	20	0.85
7	172	144	90	145	171	21	0.98
6	154	161	150	153	145	22	1.08
4	90	141	87	150	138	23	1.09
6	141	174	177	156	177	24	0.81
6	138	138	164	166	78	25	1.19
5	131	148	171	121	87	26	0.64
5	130	145	131	134	98	27	0.99
4	98	135	86	177	174	28	0.75
5	128	151	138	98	156	29	0.97
4	80	153	102	171	135	30	1.03
6	135	164	88	141	152	31	0.86
7	171	147	121	135	102	32	1.20
6	147	156	134	126	153	33	0.91
6	156	134	130	147	90	34	1.11
4	85	98	174	152	134	35	0.90
6	153	85	156	151	147	36	1.03
4	87	102	124	78	144	37	0.83
6	134	78	152	85	164	38	0.89
7	166	149	128	138	88	39	1.30
7	161	130	153	144	80	40	0.94
5	124	131	145	90	86	41	1.19
7	164	90	144	164	85	42	1.02
7	177	80	119	149	130	43	1.12
7	174	87	80	86	131	44	1.23
6	152	124	135	130	151	45	0.81
5	119	86	148	102	121	46	0.79
5	121	88	85	88	128	47	1.19
6	144	121	147	119	124	48	1.09
6	151	119	151	128	119	49	0.98
6	149	126	126	131	149	50	0.72
5	126	128	149	124	126	51	0.53

*Shaded cells refer to regression coefficients significantly different from 1.

Table 5.5.4: Pearson correlation coefficients for all 4 tests for all common treatments in CAMCORE 02 series.

	20-07-02D	20-18-02E	20-10-02A	20-10-02B	Mean
20-07-02D	1.00	0.58	0.67	0.51	0.59
p-value		<.0001	<.0001	0.0001	
20-18-02E	0.58	1.00	0.75	0.75	0.70
p-value	<.0001		<.0001	<.0001	
20-10-02A	0.67	0.75	1.00	0.73	0.72
p-value	<.0001	<.0001		<.0001	
20-10-02B	0.51	0.75	0.73	1.00	0.66
p-value	0.0001	<.0001	<.0001		
Mean	0.59	0.70	0.72	0.66	0.66

5.5.2.4 CAMCORE series 05

Amongst those treatments that differ in their response to site quality there does appear to be some moderate rank changes when considering those ranked in the top 20 (Table 5.5.5). As examples family 258 is ranked in the top 12 in all 5 tests whereas family 256 is ranked in the top 4 in 4 tests and 27th in the 5th. An examination of the Pearson correlation coefficients indicates that simple phenotypic correlations also vary from 0.68 between 20-07-05L and 20-10-05F to 0.34 between 20-07-05L and 20-10-05E2 (Table 5.5.6). The average rank correlation for all pairs of sites is 0.56. Amongst provenances, Zacualtipan (12) ranked 2nd in 20-10-05F and 6th in 20-10-05E2 whereas Conrado Castillo (8) ranked 4th in the latter test and 6th in the former (Table 5.5.7).

Table 5.5.5: The ranking of all common treatments for each individual test and the mean for all 5 tests as well as the regression coefficient (b1), as calculated in the previous section, for the CAMCORE 05 series*. Provenances included are (1) = Potrero de Monroy, (8) = Conrado Castillo, (10) = Tlacotla, (11) = Pinal de Amoles, (12) = Zacualtipan, (13) = Llano de las Carmonas and (SA) = South African genetic checks or controls.

Prov	20-07-05L	20-10-05F	20-18-05K	20-10-05E1	20-10-05E2	Fmean	Rank	b1
SA	999	256	214	999	225	256	1	1.41
12	258	11	998	251	227	999	2	1.39
12	256	254	251	256	214	251	3	1.18
SA	998	227	256	227	212	227	4	1.14
1	11	228	999	262	222	11	5	1.28
12	251	251	241	228	5	258	6	1.34
1	5	230	254	241	264	998	7	1.24
8	227	262	227	11	218	214	8	1.08
8	225	286	225	998	262	225	9	1.12
12	254	225	222	230	241	262	10	1.06
13	272	5	212	258	284	254	11	1.40
11	211	258	258	254	243	241	12	1.01
11	218	241	295	264	230	5	13	1.14
11	222	220	11	214	251	222	14	1.08

Table 5.5.5 continued....

Prov	20-07-05L	20-10-05F	20-18-05K	20-10-05E1	20-10-05E2	Fmean	Rank	b1
12	262	199	252	5	998	230	15	1.10
8	230	252	284	225	295	218	16	1.10
11	214	218	218	202	272	284	17	1.01
13	280	214	243	222	258	252	18	1.17
11	219	222	205	280	208	208	19	1.11
11	202	998	219	284	233	202	20	1.04
13	286	211	208	243	217	211	21	1.21
13	284	233	5	272	209	228	22	0.78
11	208	208	217	240	239	212	23	0.93
12	252	219	290	209	228	280	24	1.04
8	241	212	262	218	280	286	25	1.23
11	199	261	202	217	11	272	26	1.07
12	257	217	233	245	256	243	27	0.87
12	261	280	270	290	202	264	28	0.82
13	270	999	211	252	199	217	29	0.91
13	264	284	285	231	211	219	30	1.24
8	237	237	220	233	240	199	31	1.13
13	285	272	209	257	238	295	32	0.92
11	209	205	239	238	221	233	33	0.89
10	290	202	199	295	205	209	34	0.89
8	243	257	221	208	237	220	35	1.00
11	212	210	264	210	231	205	36	0.91
8	238	243	230	270	219	290	37	0.94
10	295	240	286	212	261	237	38	0.99
11	217	285	280	285	242	285	39	1.02
11	220	295	210	237	252	270	40	1.01
8	233	264	240	205	210	257	41	1.01
11	205	209	228	211	220	238	42	0.88
8	231	270	237	286	234	261	43	1.07
8	232	238	272	221	257	240	44	0.66
10	289	231	238	220	290	231	45	0.77
8	228	221	245	232	270	221	46	0.73
8	239	290	257	242	286	245	47	0.74
8	245	245	231	289	285	210	48	0.63
11	221	242	289	239	232	239	49	0.75
8	240	239	242	199	999	242	50	0.64
8	242	289	261	261	245	289	51	0.90
11	210	232	234	219	254	232	52	0.76
8	234	234	232	234	289	234	53	0.58

*Shaded cells refer to regression coefficients significantly different from 1.

Table 5.5.6: Pearson correlation coefficients for all 5 tests for all common treatments in CAMCORE 05 series.

	20-07-05L	20-10-05F	20-18-05K	20-10-05E1	20-10-05E2	Mean
20-07-05L	1.00	0.68	0.67	0.63	0.34	0.58
p-value		<.0001	<.0001	<.0001	0.0134	
20-10-05F	0.68	1.00	0.60	0.57	0.38	0.56
p-value	<.0001		<.0001	<.0001	0.0054	
20-18-05K	0.67	0.60	1.00	0.59	0.48	0.58
p-value	<.0001	<.0001		<.0001	0.0003	
20-10-05E1	0.63	0.57	0.59	1.00	0.38	0.54
p-value	<.0001	<.0001	<.0001		0.0048	
20-10-05E2	0.34	0.38	0.48	0.38	1.00	0.39
p-value	0.0134	0.0054	0.0003	0.0048		
Mean	0.58	0.56	0.58	0.54	0.39	0.53

Table 5.5.7: The ranking of all common provenances for each individual test and the mean for all 5 tests as well as the regression coefficient (b_1), as calculated in the previous section, for the CAMCORE 05 series*. Provenances included are (1) = Potrero de Monroy, (8) = Conrado Castillo, (10) = Tlacotla, (11) = Pinal de Amoles, (12) = Zacualtipan, (13) = Llano de las Carmonas and (SA) = South African genetic checks or controls.

20-07-05L	20-10-05F	20-18-05K	20-10-05E1	20-10-05E2	Pmean	Rank	b_1
SA	1	SA	SA	1	SA	1	1.18
1	12	1	1	11	1	2	1.09
12	SA	12	12	13	12	3	1.13
13	11	11	13	8	11	4	0.95
11	13	10	8	SA	13	5	0.96
8	8	13	11	12	8	6	0.82
10	10	8	10	10	10	7	0.87

*Shaded cells refer to regression coefficients significantly different from 1.

5.5.2.5 CAMCORE series 06

Amongst those treatments that differ in their response to site quality there does appear to be some moderate rank changes when considering those ranked in the top 20 (Table 5.5.8). As examples the South African 1st generation seedlot (997) was ranked 1st in 2 tests and 19th in another and vice versa family 215 was ranked 1st in the latter test and 15th in the former. An examination of the Pearson correlation coefficients indicates that simple phenotypic correlations also vary from 0.67 between 20-07-06E and 20-18-06D to 0.16 between 20-07-06E and 20-10-06B1 (Table 5.5.9). The average correlation for all pairs of sites is 0.34. Amongst provenances, Pinal de Amoles (11) ranked 1st in 20-10-06B2 and 4th in 20-07-06E whereas Conrado Castillo (8) ranked last in the latter test and 3rd in 20-10-06B1 (Table 5.5.10).

Table 5.5.8: The ranking of all common treatments for each individual test and the mean for all 4 tests as well as the regression coefficient (b_1), as calculated in the previous section, for the CAMCORE 06 series*. Provenances included are (1) = Potrero de Monroy, (8) = Conrado Castillo, (10) = Tlacotla, (11) = Pinal de Amoles, (13) = Llano de las Carmonas and (SA) = South African genetic checks or controls.

Prov	20-07-06E	20-18-06D	20-10-06B1	20-10-06B2	Fmean	Rank	b_1
SA	997	997	215	215	997	1	1.51
13	268	11	226	203	203	2	1.13
1	11	998	999	207	999	3	1.25
SA	999	203	207	5	998	4	1.31
SA	998	207	288	216	288	5	1.19
13	288	215	206	288	216	6	1.19
1	5	999	287	287	207	7	0.88
11	216	216	224	263	11	8	1.46
11	203	996	203	213	215	9	0.82
SA	996	226	213	301	268	10	1.47
13	263	287	247	206	5	11	1.24
13	287	5	229	226	287	12	0.96
11	206	206	998	997	996	13	1.12
11	207	288	278	999	206	14	0.95
11	215	213	216	276	226	15	0.80
11	213	247	11	248	213	16	0.91
13	278	246	268	278	263	17	1.00
10	301	276	246	268	278	18	0.93
13	276	271	997	292	229	19	0.88
10	292	224	277	996	276	20	0.96
13	271	278	996	201	271	21	0.95
12	248	229	263	224	248	22	0.90
8	229	268	244	998	247	23	0.79
8	226	301	248	271	301	24	0.97
13	277	248	201	229	224	25	0.69
8	247	277	271	247	246	26	0.80
8	246	263	276	246	277	27	0.91
8	224	292	5	244	292	28	0.99
8	244	201	301	277	201	29	0.66
11	201	244	292	11	244	30	0.75

*Shaded cells refer to regression coefficients significantly different from 1.

Table 5.5.9: Pearson correlation coefficients for all 4 tests for all common treatments in CAMCORE 06 series.

	20-07-06E	20-18-06D	20-10-06B1	20-10-06B2	Mean
20-07-06E	1.00	0.67	0.16	0.19	0.34
p-value		<.0001	0.4054	0.3197	
20-18-06D	0.67	1.00	0.49	0.26	0.47
p-value	<.0001		0.0058	0.1621	
20-10-06B1	0.16	0.49	1.00	0.30	0.32
p-value	0.4054	0.0058		0.1049	
20-10-06B2	0.19	0.26	0.30	1.00	0.25
p-value	0.3197	0.1621	0.1049		
Mean	0.34	0.47	0.32	0.25	0.34

Table 5.5.10: The ranking of all common provenances for each individual test and the mean for all 4 tests as well as the regression coefficient (b_1), as calculated in the previous section, for the CAMCORE 06 series*. Provenances included are (1) = Potrero de Monroy, (8) = Conrado Castillo, (10) = Tlacotla, (11) = Pinal de Amoles, (13) = Llano de las Carmonas and (SA) = South African genetic checks or controls.

20-07-06E	20-18-06D	20-10-06B1	20-10-06B2	Pmean	Rank	b_1^*
SA	SA	11	11	SA	1	1.22
1	1	SA	1	1	2	1.21
13	11	8	13	11	3	0.88
11	10	13	SA	13	4	0.99
10	8	1	10	8	5	0.77
8	13	10	8	10	6	0.92

*Shaded cells refer to regression coefficients significantly different from 1.

5.5.2.6 CAMCORE series 07

Amongst those treatments that differ in their response to site quality there does appear to be some moderate rank changes when considering those ranked in the top 20 (Table 5.5.11). As examples family 246 was ranked 8th in 1 test and last in another whereas family 203 was ranked in the top 10 in all 4 tests. An examination of the Pearson correlation coefficients indicates that simple phenotypic correlations also vary from 0.54 between 20-07-07D and 20-18-07A to 0.41 between 20-07-07D and 20-10-07B2 (Table 5.5.12). The average correlation for all pairs of sites is 0.49. Amongst provenances, little substantial rank changes were apparent (Table 5.5.13).

Table 5.5.11: The ranking of all common treatments for each individual test and the mean for all 4 tests as well as the regression coefficient (b_1), as calculated in the previous section, for the CAMCORE 07 series*. Provenances included are (8) = Conrado Castillo, (11) = Pinal de Amoles, (13) = Llano de las Carmonas and (SA) = South African genetic checks or controls.

Prov	20-07-07D	20-18-07A	20-10-07B1	20-10-07B2	Fmean	Rank	b_1
SA	997	305	999	200	999	1	1.20
SA	999	200	207	998	998	2	1.17
SA	998	996	997	215	997	3	1.30
13	269	998	215	269	200	4	1.01
13	263	203	998	249	203	5	1.11
12	249	300	200	207	305	6	1.17
11	203	999	249	999	249	7	1.12
10	305	997	305	246	207	8	0.96
11	200	226	226	287	215	9	0.85
11	207	215	203	203	263	10	1.20
13	275	287	248	226	269	11	1.17
13	287	263	287	263	287	12	1.00
10	300	249	229	229	300	13	1.02
11	215	269	206	997	996	14	1.03

Table 5.5.11 continued...

Prov	20-07-07D	20-18-07A	20-10-07B1	20-10-07B2	Fmean	Rank	b ₁
SA	997	305	999	200	999	1	1.20
SA	999	200	207	998	998	2	1.17
SA	998	996	997	215	997	3	1.30
13	269	998	215	269	200	4	1.01
13	263	203	998	249	203	5	1.11
12	249	300	200	207	305	6	1.17
11	203	999	249	999	249	7	1.12
10	305	997	305	246	207	8	0.96
11	200	226	226	287	215	9	0.85
11	207	215	203	203	263	10	1.20
13	275	287	248	226	269	11	1.17
13	287	263	287	263	287	12	1.00
10	300	249	229	229	300	13	1.02
11	215	269	206	997	996	14	1.03
SA	996	229	263	300	226	15	0.74
11	206	207	224	996	229	16	0.81
13	276	248	246	224	206	17	1.02
8	229	206	300	201	248	18	0.83
12	248	246	276	275	246	19	0.70
8	226	276	996	305	276	20	1.03
8	224	224	269	248	275	21	1.16
11	201	201	201	206	224	22	0.79
8	246	275	275	276	201	23	0.80

*Shaded cells refer to regression coefficients significantly different from 1.

Table 5.5.12: Pearson correlation coefficients for all 4 tests for all common treatments in CAMCORE 07 series.

	20-07-07D	20-18-07A	20-10-07B1	20-10-07B2	Mean
20-07-07D	1.00	0.54	0.51	0.41	0.48
p-value		0.0084	0.0136	0.0513	
20-18-07A	0.54	1.00	0.54	0.44	0.50
p-value	0.0084		0.0078	0.0363	
20-10-07B1	0.51	0.54	1.00	0.50	0.52
p-value	0.0136	0.0078		0.0144	
20-10-07B2	0.41	0.44	0.50	1.00	0.45
p-value	0.0513	0.0363	0.0144		
Mean	0.48	0.50	0.52	0.45	0.49

Table 5.5.13: The ranking of all common treatments for each individual test and the mean for all 4 tests as well as the regression coefficient (b_1), as calculated in the previous section, for the CAMCORE 06 series*. Provenances included are (8) = Conrado Castillo, (11) = Pinal de Amoles, (13) = Llano de las Carmonas and (SA) = South African genetic checks or controls.

20-07-07D	20-18-07A	20-10-07B1	20-10-07B2	Pmean	Rank	b_1
SA	SA	SA	11	SA	1	1.19
11	11	11	SA	11	2	0.98
13	8	8	13	13	3	1.04
8	13	13	8	8	4	0.79

*Shaded cells refer to regression coefficients significantly different from 1.

5.5.2.7 ICFR series

Amongst those treatments that differ in their response to site quality there does appear to be some moderate rank changes when considering those ranked in the top 20 (Table 5.5.14). As examples family 231 was ranked 7th at Graskop and 26th at Ugie whereas family 200 was ranked 9th at Ugie and 38th at Graskop. An examination of the Pearson correlation coefficients indicates that simple phenotypic correlations also vary from 0.74 between Graskop and Usutu to 0.17 between Usutu and Ugie (Table 5.5.15). The average correlation for all pairs of sites is 0.46.

Table 5.5.14: The ranking of all common treatments for each individual test and the mean for all 5 tests as well as the regression coefficient (b_1), as calculated in the previous section, for the ICFR series*.

Graskop	Bulwer	Helvetia	Usutu	Ugie	Fmean	Rank	b_1
170	149	165	3000	248	165	1	1.34
4000	170	189	4000	149	170	2	1.60
165	171	160	171	189	4000	3	1.40
3000	74	61	184	184	171	4	1.31
184	61	231	165	75	149	5	0.91
171	75	4000	13	165	184	6	1.07
231	9	248	168	74	61	7	1.17
13	160	169	189	160	189	8	0.79
61	165	149	6	200	3000	9	1.36
91	183	48	61	177	231	10	1.35
74	42	146	4	91	13	11	1.04
193	231	183	170	9	74	12	1.01
15	15	177	74	13	168	13	0.93
169	52	74	149	170	160	14	1.04
160	229	184	193	168	248	15	0.74
229	184	153	231	61	183	16	1.03
168	189	219	200	219	229	17	1.09
69	168	4	9	183	177	18	0.90
149	193	171	219	87	91	19	0.96
189	13	75	87	169	9	20	0.86
55	6000	9	48	193	169	21	1.09

Table 5.5.14 continued....

	Graskop	Bulwer	Helvetia	Usutu	Ugie	Fmean	Rank	b ₁
153	3000	229	91	72	75	22	0.88	
177	169	91	42	58	48	23	1.04	
248	4000	170	229	28	193	24	1.05	
4	244	244	177	229	4	25	1.12	
183	248	52	47	231	42	26	1.07	
244	177	168	169	52	200	27	0.67	
22	4	42	183	69	52	28	0.95	
42	219	10	248	171	87	29	0.86	
6	6	3000	15	4000	219	30	0.68	
48	200	224	52	10	146	31	0.97	
75	87	193	153	244	15	32	1.20	
87	67	67	67	22	153	33	1.20	
72	10	200	22	146	6	34	0.98	
146	48	87	55	6000	244	35	1.08	
52	28	13	224	42	69	36	0.97	
9	78	58	6000	266	55	37	1.05	
200	72	55	146	78	10	38	0.91	
10	22	266	28	55	22	39	0.94	
28	146	69	266	48	6000	40	0.83	
47	91	6000	75	15	28	41	0.78	
78	58	15	69	3000	58	42	0.71	
266	266	28	160	224	72	43	0.88	
6000	153	22	10	6	67	44	0.88	
224	55	47	72	47	224	45	0.82	
67	69	72	58	67	266	46	0.83	
58	224	6	244	4	47	47	0.77	
219	47	78	78	153	78	48	0.91	

*Shaded cells refer to regression coefficients significantly different from 1.

Table 5.5.15: Pearson correlation coefficients for all 5 tests for all common treatments in ICFR series.

	Graskop	Bulwer	Helvetia	Usutu	Ugie	Mean
Graskop	1.00	0.42	0.52	0.74	0.31	0.50
p-value		0.0031	0.0002	<.0001	0.0326	
Bulwer	0.42	1.00	0.54	0.41	0.49	0.47
p-value	0.0031		<.0001	0.0034	0.0004	
Helvetia	0.52	0.54	1.00	0.45	0.50	0.50
p-value	0.0002	<.0001		0.0012	0.0003	
Usutu	0.74	0.41	0.45	1.00	0.17	0.44
p-value	<.0001	0.0034	0.0012		0.252	
Ugie	0.31	0.49	0.50	0.17	1.00	0.37
p-value	0.0326	0.0004	0.0003	0.252		
Mean	0.50	0.47	0.50	0.44	0.37	0.46

5.5.2.8 Sappi S1 series

Amongst those treatments that differ in their response to site quality there does appear to be some quite large rank changes (Table 5.5.16). As examples family SB1 was ranked 1st in PG30

and 50th in PG29 whereas family FB8 was ranked 5th in PG29 and 44th in PG30. An examination of the Pearson correlation coefficients indicates that simple phenotypic correlations are generally quite low varying from 0.43 between PG28 and PG30 to 0.06 between PG30 and PG31 (Table 5.5.17). The average correlation for all pairs of sites is a low 0.38.

Table 5.5.16: The ranking of all common treatments for each individual test and the mean for all 4 tests as well as the regression coefficient (b_1), as calculated in the previous section, for the Sappi series 1*.

PG30	PG28	PG31	PG29	Fmean	Rank	b_1
SB1	SB6	SB6	SB4	SB6	1	1.10
MB3	SB1	SB4	FB7	SB1	2	1.52
PB86	PB118	PB40	PB122	MB3	3	1.39
FB5	PB86	FB2	PB96	SB3	4	1.05
Monmix 2	FB2	SB1	FB8	FB9	5	1.15
MB6	PB112	PB106	ZA5	PB86	6	1.36
FB9	cam22	SB3	FB9	SB4	7	0.80
PB19	PB114	SB2	SB3	FB2	8	1.08
SB3	SB3	PB116	PB90	MB6	9	1.27
PB106	PB88	ZA5	ZA4	FB5	10	1.23
PB88	FB9	P10011	SAPMIX	ZA5	11	0.92
MB2	MB6	FB8	PB100	PB122	12	1.00
SB6	MB3	PB93	cam5	cam5	13	0.92
PB122	PB122	cam21	SB2	PB19	14	1.20
cam22	PB40	MB3	cam21	PB88	15	1.23
FB2	SB5	FB3	PB85	PB114	16	1.00
PB119	PB93	Cam5	PB19	ZA4	17	0.94
PB89	PB115	FB5	PB116	PB85	18	0.93
cam11	PB116	SB5	SB6	SB2	19	0.89
SB4	PB19	PB85	PB114	PB116	20	0.87
ZA5	cam21	PB118	MB5	FB8	21	0.78
PB101	PB96	FB9	PB86	PB118	22	0.99
PB87	ZA5	PB120	FB1	SB5	23	1.02
PB97	cam5	MB5	FB5	PB93	24	1.03
PB107	ZA1	FB7	FB3	PB106	25	1.09
MB5	PB100	MB1	PB40	PB96	26	0.76
SB2	ZA4	PB107	Cam11	cam21	27	0.80
MB4	FB5	ZA4	MB4	FB7	28	0.72
ZA4	MB1	MB6	ZA1	ZA1	29	1.00
PB85	PB85	ZA1	MB6	MB2	30	1.11
cam5	PB101	PB115	FB2	cam22	31	1.22
FB1	PB107	PB96	FB4	PB101	32	1.07
ZA1	SB4	cam12	FB6	MB5	33	0.95
SB5	ZA6	MB2	Cam12	PB107	34	1.07
SAPMIX	FB8	PB114	MB3	PB40	35	0.73
FB10	MB2	PB88	PB115	PB100	36	0.83
PB90	FB6	PB89	PB101	MB1	37	1.01
PB93	PB97	ZA3	MB2	PB90	38	0.91
FB3	FB1	PB119	SB5	PB119	39	1.10
PB114	ZIMX	PB101	Cam22	cam11	40	1.02
MB1	PB119	ZA2	PB95	FB1	41	1.00

Table 5.5.16 continued....

PG30	PG28	PG31	PG29	Fmean	Rank	b ₁
PB112	MB4	cam11	P10011	PB97	42	1.10
FB7	SB2	PB108	PB118	FB3	43	0.86
FB8	SAPMIX	PB100	PB107	SAPMIX	44	0.95
PB116	PB90	FB4	PB106	MB4	45	1.04
ZIMX	ZA3	P10021	MB1	Monmix2	46	1.36
FB4	FB4	FB6	PB119	PB112	47	1.27
ZA3	FB7	PB112	PB93	PB115	48	0.82
ZA2	PB106	PB97	PB88	FB6	49	0.90
PB96	MB5	PB87	SB1	FB4	50	0.89
FB6	cam11	ZIMX	Monmix2	ZIMX	51	0.99
PB118	Monmix2	PB122	PB97	PB87	52	1.12
ZA6	PB120	FB1	ZIMX	PB89	53	1.10
cam21	P10021	PB90	ZA2	ZA6	54	1.01
PB100	PB87	PB86	ZA6	ZA3	55	1.00
PB95	PB108	PB95	PB108	P10011	56	0.70
cam12	FB3	FB10	P10021	cam12	57	0.74
P10011	PB89	ZA6	PB87	PB120	58	0.85
PB115	FB10	PB19	PB89	ZA2	59	0.90
PB120	ZA2	MB4	ZA3	FB10	60	1.09
PB40	cam12	SAPMIX	PB120	PB95	61	0.79
P10021	P10011	cam22	FB10	P10021	62	0.80
PB108	PB95	Monmix2	PB112	PB108	63	0.66

*Shaded cells refer to regression coefficients significantly different from 1.

Table 5.5.17: Pearson correlation coefficients for all 4 tests for all common treatments in Sappi series s1.

	PG30	PG28	PG31	PG29	Mean
PG30	1.00	0.43	0.06	0.16	0.22
p-value		0.0004	0.6143	0.2024	
PG28	0.43	1.00	0.36	0.23	0.34
p-value	0.0004		0.0035	0.0659	
PG31	0.16	0.23	0.29	1.00	0.47
p-value	0.2024	0.0659	0.0218		
PG29	0.06	0.36	1.00	0.29	0.48
p-value	0.6143	0.0035		0.0218	
Mean	0.22	0.34	0.48	0.47	0.38

5.5.2.9 Sappi S2 series

Only 2 treatments differed in their response to site quality and the rank changes correspond to the two sites that the tests are planted on (Table 5.5.18). PG35 and 33 are planted adjacent to each other at Helvetia, Mpumalanga province and PG34 and 36 at Pinewoods, KZN. Family ZA6 is ranked above PB116 in PG33 and 35 and vice versa at PG34 and 36. An examination of the Pearson correlation coefficients indicates that simple phenotypic correlations are generally quite low varying from 0.53 between PG34 and PG35 to 0.26 between PG34 and PG36 (Table 5.5.19). The average correlation for all pairs of sites is a low 0.35.

Table 5.5.18: The ranking of all common treatments for each individual test and the mean for all 4 tests as well as the regression coefficient (b_1), as calculated in the previous section, for the Sappi series 2*.

PG35	PG33	PG36	PG34	Fmean	Rank	b_1
PB89	PB86	PB96	PB86	PB102	1	1.33
PB112	PB102	PB102	SAPMIX	PB86	2	1.07
PB102	PB90	PB106	PB85	PB96	3	0.97
PB96	SAPMIX	ZIMX	PB118	SAPMIX	4	0.97
ZA4	ZA5	PB110	PB84	PB90	5	1.38
PB90	PB112	ZA1	Monmix2	PB112	6	1.59
PB118	PB92	PB94	PB92	PB110	7	1.05
PB92	PB110	PB95	PB19	PB92	8	1.29
PB119	PB96	PB113	PB104	PB118	9	1.04
PB86	ZA3	PB107	PB114	ZA5	10	1.21
PB122	PB113	PB119	PB112	PB85	11	0.84
Monmix 2	PB109	PB109	PB102	PB89	12	1.23
PB114	PB115	PB90	ZIMX	PB94	13	0.96
PB85	PB108	PB88	PB101	PB119	14	1.04
PB94	PB114	PB86	PB120	PB114	15	1.13
PB110	PB101	PB116	PB106	PB113	16	1.22
SAPMIX	ZA2	PB89	PB96	PB106	17	0.74
PB113	PB118	ZA2	PB89	ZA3	18	1.13
ZA5	PB93	PB19	ZA1	Monmix2	19	0.98
PB88	ZA1	PB99	PB110	ZIMX	20	0.74
ZA3	PB104	PB120	PB119	ZA2	21	0.96
PB84	PB99	ZA3	PB94	ZA4	22	1.23
PB117	ZA6	ZA5	PB8	PB19	23	0.77
ZA2	PB106	SAPMIX	ZA2	PB88	24	1.03
PB19	PB107	PB85	ZA4	PB109	25	0.88
PB91	PB105	Monmix2	PB116	PB101	26	0.90
ZA6	PB94	PB101	PB90	ZA1	27	0.59
PB106	PB119	PB114	PB117	PB116	30	0.78
PB104	PB97	PB122	PB122	PB107	31	0.71
PB101	ZIMX	ZA4	PB107	PB115	32	1.04
PB97	PB85	PB91	ZA3	ZA6	33	1.16
PB8	Monmix2	PB8	PB105	PB93	34	0.92
PB116	PB111	PB93	PB88	PB122	35	1.12
PB120	ZA4	PB84	PB109	PB120	36	0.65
PB115	PB87	PB118	PB108	PB108	37	1.26
PB93	PB19	PB104	ZA6	PB105	38	0.81
PB109	PB84	ZA6	PB97	PB99	39	0.90
PB107	PB91	PB117	PB95	PB95	40	0.60
PB95	PB120	PB92	PB87	PB117	41	0.99
PB99	PB89	PB112	PB115	PB97	42	1.08
ZA1	PB95	PB97	PB113	PB8	43	0.72
PB105	PB122	PB108	PB99	PB91	44	1.21
PB87	PB117	PB87	PB91	PB87	45	0.85
PB111	PB8	PB111	PB111	PB111	46	1.19

*Shaded cells refer to regression coefficients significantly different from 1.

Table 5.5.19: Pearson correlation coefficients for all 4 tests for all common treatments in Sappi series S2.

	PG33	PG34	PG35	PG36	Mean
PG33	1.00	0.32	0.36	0.32	0.33
p-value		0.0284	0.0142	0.0292	
PG34	0.32	1.00	0.53	0.26	0.37
p-value	0.0284		0.0002	0.0774	
PG35	0.36	0.53	1.00	0.29	0.39
p-value	0.0142	0.0002		0.0542	
PG36	0.32	0.26	0.29	1.00	0.29
p-value	0.0292	0.0774	0.0542		
Mean	0.33	0.37	0.39	0.29	0.35

5.5.3 Discussion

5.5.3.1 The difficulty in considering rank changes lies in the way to quantify and compare the extent of these rank changes. Several methods were considered including the estimation of Pearson correlation coefficients, as well as examination of the data to determine the amount and extent of these changes in rank.

5.5.3.2 Amongst the interactive genotypes some rank changes were apparent, although certainly not in all cases. In addition, some of those genotypes, although interactive, represent the poorer performing genotypes and would thus not challenge those genotypes which performed well throughout. Generally, as a subjective description, amongst the imported Mexican material rank changes could be described as low to moderate whereas amongst the South African progeny test series, with the exception of Sappi S2, the rank changes could be described as moderate to strong. The most dramatic rank changes were apparent amongst the 2nd generation Sappi families.

5.5.3.3 A look at phenotypic correlations per series supports the general trend observed above. These correlations are family mean correlations, which are measuring the same thing as the aggregate Type B genetic correlations. The difference is that these correlations have error noise, and are therefore biased lower compared to the aggregate Type B genetic correlations reported earlier. They do however, represent the actual rank changes that are occurring and should be only be considered as a tool in examining the actual performance of the individual genotypes. Ultimately it should be noted that it is the aggregate Type B genetic correlations that are giving a more unbiased measure of the real correlation of interest.

5.5.3.4 The average correlations for the CAMCORE material range from 0.34 (series 06) to 0.66 (series 02) with the 'average' for all the Mexican material being 0.51. The ICFR average was 0.46 and the Sappi S1, 0.35. These are quite clearly lower than the Type genetic correlation estimates alluded to earlier. By comparison, the Type B genetic correlations vary from 0.61 (series 06) to 0.75 (series 01) with the average for the Mexican material being 0.68. Similarly, the South African material has much higher Type B genetic correlation estimates than phenotypic correlation estimates. Nevertheless, the trends are similar.

5.5.3.5 Is there a relationship between the level of improvement, and instability? Perhaps the level of adaptation to local environment, speeded up by artificial selection, may be producing 'specialized' genotypes? Alternatively, are any trends simply influenced by the choice of genotypes and / or environments in each series?

5.6 Differences in response amongst different populations across similar environments

5.6.1 Introduction

Different populations of genotypes may react differently to a given set of environments (Barnes et al., 1984). In this study, each trial series actually represents a diverse range of populations. The average r_{Bg} estimated for each trial series across sites differed and varied from 0.79 for the ICFR tests to 0.62 for the Sappi trials (Tables 5.2.3, 5.2.4 & 5.2.5) with the CAMCORE tests ranging between these 2 extremes. These differences could of course reflect differences in the diversity of sites sampled. However, in any population different sets of genes are present that may interact in different ways with the environment. The CAMCORE material was sampled over a large area of the natural range of *P. patula* in Mexico and certainly would represent a diverse sample of populations within the species. Five of these series were planted over 4 similar sites which allows a comparison between the 4 different populations across site.

5.6.2 A comparison between 4 different populations across 4 sites

CAMCORE trial series 01, 02, 05, 06, 07 were all planted across 4 sites where a test from each series planted adjacent to each other at each site (Table 5.6.1). The data set does afford a comparison between 5 CAMCORE trial series across 4 sites ensuring a nicely stratified data set where control over both the genetics and environment is maintained.

Table 5.6.1: Trial, site & climate details for CAMCORE series 01, 02, 05, 06, 07 planted across 4 sites in South Africa. These tests were planted together under similar conditions in the same season.

Series	Test	Planted	Location	Site Description	Provenances sampled*
01	20-10-01A	Jan, 1991	Safcol Tweefontein	Alt. = 1182m	1, 2, 3
02	20-10-02A	Jan, 1991	plantation,	MAP = 1274mm	1, 4, 5, 6, 7
05	20-10-05E1	Jan, 1991	Mpumalanga	MAT = 17.5°C	1, 8, 10, 11, 12, 13
06	20-10-06B1	Jan, 1991			1, 8, 10, 11, 13
07	20-10-07B1	Jan, 1991			1, 8, 11, 13
01	20-10-01B	Feb, 1991	Safcol Jessievale	Alt. = 1716m	1, 2, 3
02	20-10-02B	Feb, 1991	plantation,	MAP = 921mm	1, 4, 5, 6, 7
05	20-10-05E2	Feb, 1991	Mpumalanga	MAT = 14°C	1, 8, 10, 11, 12, 13
06	20-10-06B2	Feb, 1991			1, 8, 10, 11, 13
07	20-10-07B2	Feb, 1991			1, 8, 11, 13
01	20-07-01L	Dec, 1990	Sappi Maxwell	Alt. = 1405m	1, 2, 3
02	20-07-02D	Dec, 1990	plantation, KZN	MAP = 817mm	1, 4, 5, 6, 7
05	20-07-05L	Dec, 1990		MAT = 16°C	1, 8, 10, 11, 12, 13
06	20-07-06E	Dec, 1990			1, 8, 10, 11, 13
07	20-07-07D	Dec, 1990			1, 8, 11, 13
01	20-18-01J	Feb, 1991	Mondi Commonage	Alt. = 1480m	1, 2, 3
02	20-18-02E	Feb, 1991	plantation, North	MAP = 757mm	1, 4, 5, 6, 7
05	20-18-05K	Feb, 1991	Eastern Cape	MAT = 14.5°C	1, 8, 10, 11, 12, 13
06	20-18-06D	Feb, 1991			1, 8, 10, 11, 13
07	20-18-07A	Feb, 1991			1, 8, 11, 13

*Provenances included are (1) = Potrero de Monroy, (2) = Ingenio del Rosario, (3) = Corralitla, (4) = El Manzanal, (5) = El Tlacuache, (6) = Ixtlan, (7) = Santa Maria Papalo, (8) = Conrado Castillo, (10) = Tlacotla, (11) = Pinal de Amoles, (12) = Zacualtipan, (13) = Llano de las Carmonas

Table 5.6.2: Aggregate family – provenance Type B genetic correlation estimates for volume (using standardized data), for 6 pairs of sites where CAMCORE trial series 01, 02, 05, 06 and 07 were planted together under similar conditions in the same season.

Pairs	Code	s01*	s02	s05	S06	s07	Mean	Range
Tweefontein Jessievale H13	TJ	0.86	0.97	0.76	0.75	0.90	0.85	0.75 – 0.97
Tweefontein Maxwell	TM	0.74	0.72	0.74	0.28	0.44	0.58	0.28 – 0.74
Tweefontein Commonage	TC	0.47	0.68	0.65	0.69	0.86	0.67	0.47 – 0.86
Jessievale H13 Maxwell	JM	0.89	0.57	0.49	0.54	0.27	0.55	0.27 – 0.89
Jessievale H13 Commonage	JC	0.94	0.91	0.77	0.80	0.62	0.81	0.62 – 0.94
Maxwell Commonage	MC	0.55	0.47	0.76	0.60	0.63	0.60	0.47 – 0.76
	Mean	M	0.74	0.72	0.695	0.61	0.62	0.68
	Range		0.47	0.47	0.49	0.28	0.27	0.55
			0.94	0.97	0.77	0.8	0.9	0.85

*Site at Jessievale for this series not adjacent but rather around 5 km apart from the others.

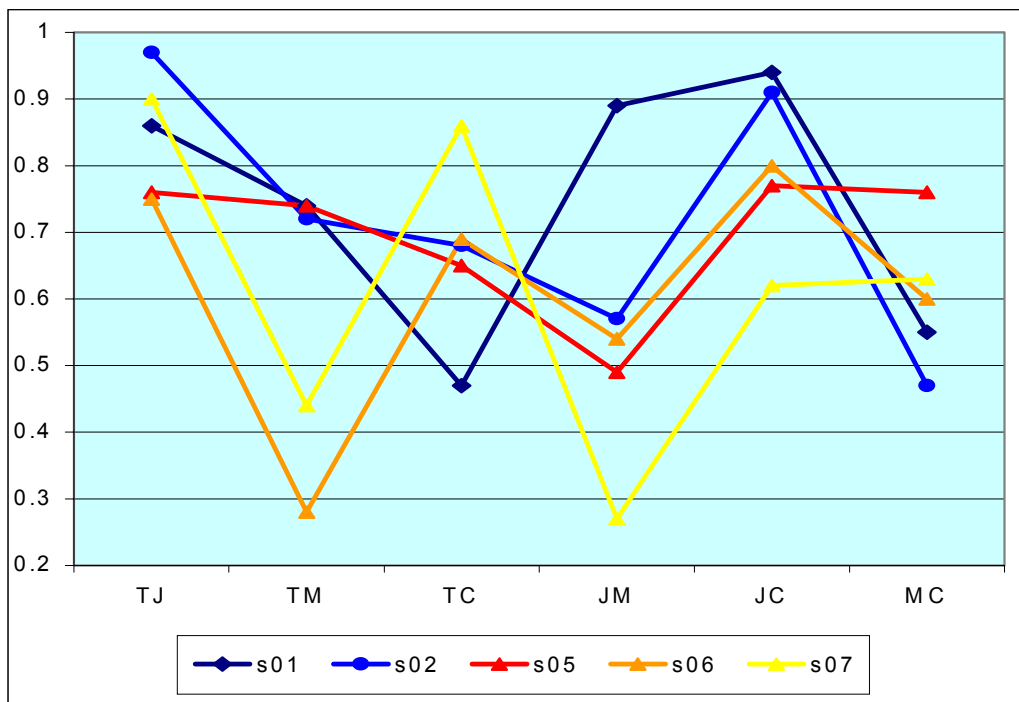


Figure 5.6.1: Aggregate family – provenance type b genetic correlation estimates for volume (using standardized data), for 6 pairs of sites where CAMCORE trial series 01, 02, 05, 06 and 07 were planted together under similar conditions in the same season.

5.6.3 Discussion

5.6.3.1 There is considerable variation amongst populations for the estimated Type B genetic correlations for each pair of sites (Table 5.6.2). The estimated Type B genetic correlations for each of the 5 trial series has a range from 0.29 (0.47 – 0.76) for the Maxwell – Commonage pair (MC) to 0.62 (0.27 – 0.89) for the Jessievale – Maxwell pair (JM). This range in variation in the estimates in most cases represents greater variation than between pairs of sites within individual trial series. This does cast some doubt on the ability to use estimates of Type B genetic correlations from a range of populations to attempt to predict the effect of environment on genotypic responses.

5.6.3.2 In addition the trends are not always the same. For example, for 3 of the trial series (01,02 & 05), the estimates of the r_{Bg} 's decreases from TM to TC, whereas for the other 2 (06 & 07) they increase dramatically (Figure 5.6.1). The 3 series (05, 06 & 07) do not differ substantially in the provenances sampled and do tend to follow similar trends. The other 2 series (01 & 02) represent very different provenances and do differ somewhat in their genotypic responses. There are, however, some relative responses that appear similar throughout all the series. These similarities do include generally high correlations for all pairs for the TJ and JC comparisons and lower ones for the TM, JM and MC.

CHAPTER 6: DETERMINATION OF THE KEY ENVIRONMENTAL VARIABLES THAT CONTRIBUTE TO THE GxE AND DEVELOPMENT OF BREEDING AND DEPLOYMENT MODELS FOR *P. PATULA*

Chapter Summary

6.1 Introduction

6.2 A look at some possible environmental variables

6.3 A site factor study looking at the sites in the present study

6.4 The use of Type B genetic correlation estimates to group environments

6.5 Towards a tentative GxE regionalisation model

6.1 Introduction

In this chapter the focus switches to the environment. The previous chapters have focused on quantifying the level of GxE and attempting to ascertain the patterns of interactions as they occur in *P. patula* in Southern Africa. Useful genetic parameters such as type B genetic parameters have been estimated for a range of sites. These estimates should now be considered in the context of the type of environments tested.

6.2 A look at some possible environmental variables

6.2.1 *P. patula* and its environment in Southern Africa

6.2.1.1 It is important to begin by listing and discussing the sort of environmental variables that affect *P. patula* growth and may be important in causing GxE in the species. A brief discussion of the species in the context of its natural habitat and environment in Southern Africa follows.

6.2.1.2 In Southern Africa, large areas are unsuitable for plantation forestry, and in many previous studies of tree growth in the sub-region climatic factors have consistently been identified as being important (King, 1951), (Poynton, 1971), (Schonau and Schulze, 1984). In addition, soil factors have also been identified as key determinants of tree growth (Schonau and Fitzpatrick, 1981), (Grey et al., 1987). Furthermore, the region is characterized as generally having high evaporative demand and limited soil water availability (Roberts, 1994). Finally, many of the forest soils of the region are inherently low in fertility since they occur on ancient weathering surfaces in high rainfall areas (Olbrich et al., 1997).

6.2.1.3 The type of environments in which *P. patula* grows in Mexico should also provide valuable clues, in particular those that seem to regulate the boundaries of the distribution (Vela, 1980), (Dvorak et al., 2000). The growth of the species mirrors the occurrence of the fog and cloud belts, and within this it may be further defined by soil depth. It is found in an elevation band varying from 1500 to 3000m, depending on latitude and aspect. At the higher elevations, humidity decreases, whereas at lower altitudes temperatures increase and fog and rainfall decrease. As a consequence, at both extremes the species is replaced by other conifers and broadleaf trees. In those areas where the species grows well, the soils tend to be deep and well drained. However, even in this cloud belt region, as soils get shallower, *P. patula* is outcompeted by other species, like *P. teocote*.

6.2.1.4 The species requirements within Southern Africa have been considered by many authors (Kotze, 1926), (Poynton, 1957), (Poynton, 1966), (Barrett and Mullin, 1968), (Esterhuysen, 1985), (Schonau and Grey, 1987), (Schutz, 1994). Generally, the requirements have included a reference to rainfall or moisture availability, altitude, adaptation to frost and snow, a moderate drought tolerance, the presence of mist, a preference for moderate, to deep, well drained soils and a wide tolerance to exposure. Most recently, the species niche for *P. patula*, has been defined as requiring mean annual temperatures of between 12 and 18°C and an annual rainfall of between 700mm at high elevations, to 950mm elsewhere (Morris and Pallett, 2000).

6.2.2 Site factor studies as an indication of potential environmental variables

6.2.2.1 Site factor studies seek to determine the quantitative relationships between measured variables and tree growth (Louw, 1999). It is important to emphasize that the site factors assessed rarely measure the primary influences on tree growth adequately. Factors such as light intensity and duration, temperature, water and CO₂ availability are likely to be of prime importance but are not easily measured (Kozłowski and Pallardy, 1996). Nevertheless, it is assumed that these secondary factors are to some extent correlated with the primary ones. Several such studies have been carried out with *P. patula* and these should be utilized as a starting point in any GxE study (Castanos, 1962), (Evans, 1974), (Grey, 1979), (Schonau and Wilhelmij, 1981), (Schutz, 1990), (Louw, 1995), (Zwolinski et al., 1998) (Table 6.2.1).

6.2.2.2 All of these studies have used linear regression analysis to relate a wide spectrum of environmental factors to tree growth (Louw, 1999). Many of these studies have identified topography (altitude, aspect and terrain position) as being of prime importance, followed by soil information (geology, effective rooting depth). These sorts of studies should give us some indication as to which variables should be considered.

6.2.2.3 These studies do, however, have a number of shortcomings and these should be kept in mind when considering the various factors identified. Some of these considerations are listed below:-

1. The models generally only work well when considering a specific, limited area. In this GxE study the growth of a range of genotypes is considered over a much larger area, encompassing the range of sites planted to *P. patula* within Southern Africa.
2. The models do not measure primary influences on tree growth. As far as possible, consideration should be given to the relevance of the factors selected, to the growth of trees in that environment.

3. Many of the factors identified are correlated with each other and this introduces the problem of multicollinearity. This can clearly be seen in many of these studies and is almost unavoidable when considering empirical data. This problem will clearly be an issue in this study and needs to be considered when selecting variables.

Table 6.2.1: A summary of the environmental variables identified in site factor studies carried out with *Pinus patula*.

Study	Region of study	Environmental variables	Coefficient of determination (R^2)
(Castanos, 1962)	Mexico	Total soil depth, aspect, elevation	0.53
(Evans, 1974)	Usutu Forest, Swaziland	Elevation above sea level, distance from ridge, soil set	0.84
(Grey, 1979)	Umzinkulu district of KwaZulu-Natal	Elevation above seal level, percentage distance from ridge, slope shape, aspect, land surface, soil chemical factors associated with A horizon	0.42 – 0.48
(Schonau and Wilhelmij, 1981)	KwaZulu-Natal midlands	Mean annual precipitation, South African classification of soil form	0.21 – 0.30
(Schutz, 1990)	Mpumalanga escarpment	Geology, effective soil depth, Ca in top soil, volume of stones in B horizon, Altitude, fine sand in A horizon, terrain position	0.80
(Louw, 1995)	Mpumalanga escarpment	Terrain position, geology, effective soil depth, driest quarter precipitation	0.74
(Zwolinski et al., 1998)	North Eastern Cape	Soil available water, rainfall	0.57 – 0.80*

* Used a combination of *P. patula*, *P. elliottii* and *P. radiata* for the study

6.2.2.4 In addition to these site factor studies, a number of other climatic factors have been identified and used for developing site index predictions for the species (Strydom, 2000). These include, in addition to mean annual precipitation, driest quarter precipitation and maximum temperature of the hottest month. These sorts of variables have been used successfully to predict *P. patula* site index on Sappi landholdings. A combination of mean maximum temperature in the hottest month, mean precipitation in the wettest month and in the driest quarter and a climate index for August derived from the mean precipitation divided by the mean maximum temperature in that month, explained around 69% of the variation in Site index (Pallett, 2001).

6.2.2.5 It is desirable that any environmental variables selected in this study should attempt to take cognizance of the following two criteria: 1) They should be relatively easy to calculate and predict for any site within the area of interest. 2) They should be biologically meaningful and relevant to tree growth or at least be correlated with a variable that may be seen to be relevant.

6.2.3 A list of potential key environmental variables

6.2.3.1 The environmental variables that were considered in this study are listed along with brief discussions as to their relevance and reasons for being considered. All factors considered needed to be easily obtainable and reproducible across all sites in the region.

6.2.3.2 Site quality is not strictly speaking an environmental variable but is a reflection of the site growth potential and is an obvious candidate when considering those factors that may influence GxE. Indeed, site index has been found to be important as a predictor of GxE in *P. elliotii* in the SE USA. (Hodge and White, 1992). In addition, it was possible to calculate site index from each of the test sites within the study using the growth of the trees within the trials.

6.2.3.3 Factors associated with rainfall have been shown to be important in the growth of *P. patula*. (Schonau and Wilhelmij, 1981), (Louw, 1995), (Morris and Pallett, 2000) , (Strydom, 2000). This factor includes not only annual precipitation but also any variation on specific rainfall in any particular season or month, for example, mean precipitation in the driest quarter, mean precipitation in the wettest month, and indeed in all months of the year.

6.2.3.4 Factors associated with topography have been shown to be good indicators of site quality for the species in almost all the site factor studies (Table 6.2.1). These include elevation above sea level, aspect and terrain position. Most of these factors are likely to be correlated with other more primary factors such as water availability, temperature and solar radiation. Thus, it is these latter variables that are considered further.

6.2.3.5 Factors associated with temperature were also utilized. These were considered important despite the fact that none of these had been identified from any of the previous site factor studies with *P. patula* in the region. However, as already mentioned, topographic factors such as elevation will be strongly correlated with temperature. In addition, the rate of critical physiological processes driving tree growth, such as respiration and photosynthesis are linked to a temperature range which is specific to species and indeed genotype (Kozlowski and Pallardy, 1996). The latest definition for the species niche in the region also identifies an annual temperature of 18°C or lower as critical (Morris and Pallett, 2000).

6.2.3.6 Many of the site factor studies identified some soil characters as being important in the growth of *P. patula* (Table 6.2.1). However, many of the authors also found that these were often of relatively minor importance in predicting tree growth. In addition, many were correlated with other variables, in particular those related to topography (Evans, 1974), (Grey, 1979), (Schutz,

1990). A good example of these latter correlations was the obvious relationship between geology and elevation.

6.2.3.7 The issue of soils is certainly likely to be important, but is not utilized further in this study for a number of reasons:-

1. As mentioned above it seldom has been shown to be a major factor in any site growth study with *P. patula*. This is despite the fact that these studies, have often involved extensive analyses of soil physical and chemical properties, over relatively small and uniform areas.
2. This GxE study is looking specifically at genetic parameter estimates which are relatively imprecisely measured, and, in addition, sampled over an extensive part of the *P. patula* range in the region on a limited number of sites. It is likely that this would decrease the likelihood of finding meaningful relationships with the soil parameters available.
3. The sort of soil characteristics that were generally highlighted from the site factor studies were related to soil depth or available soil water capacity. These are undoubtedly likely to be important; however, to define soil depth or available soil water capacity for tree growth has been extremely difficult and more so over a geographically diverse area.
4. Soil surveys were carried out in a number of the tests in this study and relatively large changes in these latter characteristics were seen even within these test sites. Thus, soils are often extremely variable over small distances and using them in any prediction or model would be problematic and fraught with error.

6.2.3.8 It is important to remember that the primary productivity of tree growth is related to the rates of photosynthesis and this physiological process is affected by a range of environmental variables such as light, temperature, CO₂ concentration of the air, water supply, air humidity amongst many others (Kozlowski and Pallardy, 1996). Quite clearly, when considering empirical data such as those available, many of these factors would be difficult to measure for all environments. A number of factors that were accessible and repeatable were considered in the hope that some would have predictive power.

6.3 A site factor study looking at the sites in the present study

6.3.3 Introduction

6.3.3.1 A site factor study seeks to establish a functional relationship between the dependent variable (a measure of the growth of trees) and subjectively selected independent environmental variables (Grey, 1983). In this case, the dependent variable selected was Site Index. The objective was to determine, within the scope of the region and sites available, which

environmental variables had significant impacts on tree growth. It was felt that this process would serve as a useful screening study in helping to determine those factors that may have significance in driving the GxE interactions related to tree growth.

6.3.4 Determination of Site Index and Site quality for each test

6.3.4.1 Site index was selected as the best measure of tree growth as it is based on the dominant height of trees in a stand and is little affected by variations in stand density. This latter property means it is a useful parameter for measuring the productive potential of a site.

6.3.4.2 The estimation of top height.

An estimation of site index requires the elucidation of top height for a stand of trees. Top height was calculated, using a procedure developed for the species in South Africa, as follows (Bredenkamp, 1993)

$$\ln H = b_0 + b_1 / D$$

where H = total tree height (m)

D = breast height diameter (cm)

ln = natural logarithm, base e

b_0, b_1 = coefficients to be estimated.

In addition to the above equation several other requirements needed to be met;

1. The sample should include no less than 30 height/dbh pairs for the estimation of the coefficients b_0 and b_1
2. The top height will be found by substitution of D with the quadratic mean diameter of the 20% largest trees included in the sample.
3. Trees should be selected at random within the diameter strata.

The choice of the genetic checks in most cases met the above criteria (Table 6.3.1) and in most cases more than one seedlot was available for each test.

6.3.4.3 The calculation of Site Index at base 15 years.

Site index is defined as the dominant stand height attained at a specified reference age (von Gadow and Bredenkamp, 1992). Height-based methods of site quality assessment rely on height-growth curves with age in order to project dominant height in stands not measured at reference age to a site index at reference age. In this study, non-linear height on age relationships, using the Chapman-Richards growth model, were used. Functions specifically derived for KwaZulu-Natal (South) and Mpumalanga (North) were used for *P. patula* to project a measured dominant height for each site to a standard reference age to determine site index (Harrison, 1991). A reference age of 15 years was used. Tree functions derived for KwaZulu-

Natal were also utilized for those sites further south in the North-eastern Cape. This latter assumption may introduce some error as tree growth in this latter region may differ significantly from the other regions.

6.3.4.3 Site index was calculated for each genetic check separately in each test. All the dbh and heights for all trees in all replications for each entry was used. This yielded around 20 – 40 trees per genetic entry with some extremes outside of this range (Table 6.3.1). In most cases 3 separate site indices were calculated for each test, i.e. once for each of the genetic checks. The average of these three calculations was used as the estimate of site index for that specific test (Table 6.3.1). In all cases the oldest age of assessment available was utilized for the Site Index calculations. These ages ranged from 4 to 10 years of age.

6.3.4.4 The site indices, when measured across many sites can be divided into site quality classes. A site quality class has an equal but limited range of dominant height, usually 2 or 3 m (Philip, 1994). In this case the tests were assigned to 5 site quality classes defined according to the site index calculated. The site quality classes were classified as follows SQ1 = 24.1-27.0m, SQ2 = 21.1 – 24.0m, SQ3 = 18.1 – 21.0m, SQ4 = 15.1 – 18.0m, SQ5 = 12.1 – 15.0m (Pallett, 2001).

6.3.4.5 The result was that Site Indexes at a reference age of 15 years (SI) were calculated for a range of sites. All of these sites represented tests that were also included in the GxE study. In addition, each site was assigned into a site quality class based on the Site Index estimated for that test (Table 6.3.1).

Table 6.3.1: Site index, and numbers of trees used to calculate site index (Tnr.) for unimproved seedlots (SI-U), mixed 1st generation clonal seed orchard seedlots (SI-1), mixed 2nd generation clonal seed orchard seedlots (SI-2) and the average site index of all three per test (SI-Av). Included is a classification of site quality class (SQ) and the ranking of each test based on site index (Rk).

Series	Test	TNr.	SI-U	Tnr.	SI-1	Tnr.	SI-2	Age	SI-Av.	SQ**	Rk
CAM06	20-07-06E	50	26.3	47	27.5	43	26.7	8	26.8	1	1
FAO	MAXWELL	91	24.9	*	*	83	27.4	10	26.2	1	2
CAM08	20-07-08C	40	25.1	*	*	34	26.1	5	25.6	1	3
CAM01	PV34C	24	24.6	23	26.3	22	24.5	8	25.1	1	4
CAM01	20-07-01L	51	24.0	43	25.4	48	25.4	8	24.9	1	5
FAO	GOODHOPE	20	23.2	22	25.3	22	25.3	8	24.6	1	6
CAM05	20-07-05L	49	24.7	49	25.6	48	22.5	8	24.3	1	7
AM06	20-18-06D	40	23.3	43	23.7	40	24.0	8	23.7	2	8
CAM03	20-10-03A1	51	22.6	41	23.7	49	24.4	8	23.6	2	9
CAM05	20-18-05K	38	22.8	47	23.7	43	23.9	8	23.5	2	10
CAM01	20-18-01J	50	22.8	50	23.6	51	23.3	8	23.2	2	11
CAM01	PV34B	21	22.0	23	23.7	22	22.8	8	22.8	2	12
CAM05	20-10-05F	*	*	42	22.8	37	22.8	8	22.8	2	13
CAM07	20-18-07A	49	21.6	38	23.8	42	23.0	8	22.8	2	14
FAO	WILGEBOOM	18	22.8	*	*	*	*	8	22.8	2	15

Table 6.3.1 continued.....

Series	Test	TNr.	SI-U	Tnr.	SI-1	Tnr.	SI-2	Age	SI-Av.	SQ**	Rk
CAM07	20-07-07D	50	22.4	46	22.9	46	22.8	8	22.7	2	16
FAO	MAGSLEIGH	24	22.4	22	21.8	24	23.1	8	22.4	2	17
CAM02	20-18-02E	41	21.9	45	22.6	41	22.5	8	22.3	2	18
CAM04	20-07-04C	50	20.9	46	21.9	48	22.2	8	21.7	2	19
SAPPI_S1	PG28	52	21.6	27	20.7	30	22.3	5	21.5	2	20
ICFR	BULWER	32	23.7	28	20.4	25	20.4	6	21.5	2	21
CAM05	20-10-05E1	52	19.8	47	21.8	50	22.4	8	21.3	2	22
CAM01	20-10-01B	37	21.0	30	21.3	28	21.6	8	21.3	2	23
CAM02	20-07-02D	49	19.6	44	22.0	48	22.0	8	21.2	2	24
SAPPI_S1	PG30	37	20.4	30	21.3	25	21.5	5	21.1	2	25
CAM04	20-10-04A2	35	21.5	38	21.1	31	19.7	5	20.8	3	26
CAM10	20-07-10B	46	20.4	43	20.4	45	21.5	5	20.8	3	27
CAM02	20-10-02A	44	20.7	37	20.7	37	20.8	8	20.7	3	28
CAM03	20-10-03A2	26	20.9	37	21.5	34	19.8	8	20.7	3	29
ICFR	GRASKOP	22	20.2	20	20.6	16	21.4	6	20.7	3	30
CAM01	20-10-01A	52	19.7	46	21.6	41	20.7	8	20.7	3	31
CAM06	20-10-06B1	47	19.5	44	20.7	47	21.8	8	20.7	3	32
FAO	JESSIEVALE	30	19.8	*	*	20	21.0	8	20.4	3	33
SAPPI_S1	PG31	38	18.9	19	22.9	21	19.2	5	20.3	3	34
CAM09	20-07-09B	48	20.5	42	20.0	*	*	5	20.3	3	35
CAM15	20-07-15E	48	20.5	21	19.8	*	*	4	20.2	3	36
CAM07	20-10-07B1	49	19.6	41	20.4	43	19.9	8	20.0	3	37
CAM04	20-10-04A1	50	19.2	29	20.5	48	20.0	8	19.9	3	38
ICFR	HELVETIA	30	19.3	26	18.9	24	19.8	6	19.3	3	39
CAM07	20-10-07B2	39	18.4	25	18.5	30	19.3	8	18.7	3	40
ICFR	USUTU	58	17.1	29	20.4	27	18.7	6	18.7	3	41
FAO	WITKLIP	26	18.6	*	*	*	*	8	18.6	3	42
FAO	TWEEFONTEIN	24	18.5	*	*	*	*	8	18.5	3	43
CAM09	20-18-09A	47	18.6	45	18.3	*	*	5	18.5	3	44
CAM06	20-10-06B2	41	18.3	32	18.5	36	18.5	8	18.4	3	45
CAM01	20-18-01H	45	18.1	36	18.1	43	18.5	5	18.2	3	46
CAM08	20-18-08B	47	18.3	42	17.7	*	*	5	18.0	4	47
CAM05	20-10-05E2	35	18.5	35	17.7	29	17.1	8	17.8	4	48
CAM02	20-10-02B	36	17.5	34	17.9	28	17.9	8	17.8	4	49
CAM10	20-10-10C	51	17.6	45	17.6	*	*	5	17.6	4	50
ICFR	UGIE	52	16.8	21	16.6	24	17.1	6	16.8	4	51
CAM08	20-10-08A*	37	15.9	42	16.4	*	*	5	16.2	4	52
CAM15	R 203	*	*	*	*	29	16.0	4	16.0	4	53
SAPPI_S2	PG35*	24	16.2	23	16.6	22	15.2	4	16.0	4	54
SAPPI_S1	PG29	49	14.5	27	16.2	21	17.0	5	15.9	4	55
SAPPI_S2	PG33*	19	14.0	18	15.3	21	16.5	4	15.3	4	56
SAPPI_S2	PG36*	15	15.3	15	14.8	17	14.5	4	14.9	5	57
SAPPI_S2	PG34*	14	14.7	17	14.2	11	15.1	4	14.7	5	58
CAM15	20-10-15L	29	13.1	29	14.9	*	*	3	14.0	5	59

*Tests where seedlots other than those labelled were used (20-10-08A both seedlots were unimproved; PG33-36 no unimproved seedlots available, two 2nd gen seedlots used;

**Site quality class classified for a range of site indexes as follows SQ1 = 24.1-27.0, SQ2 = 21.1 – 24.0, SQ3 = 18.1 – 21.0, SQ4 = 15.1 – 18.0, SQ5 = 12.1 – 15.0 (Pallett, 2001).

6.3.5 Site Factor Study

6.3.5.1 The dependent variable for this site factor study was Site index at reference age 15(SI) and as has been calculated in the previous section (Table 6.3.1). A large number of independent environmental variables were utilized in this study. These are presented in table 6.3.2.

Table 6.3.2: Selected environmental variables used as independent variates for the site factor study.**

Key	Units	Range		Explanation
LONG	Degrees	28.18	30.98	Degrees longitude east
LAT	Degrees	24.78	31.18	Degrees latitude south
ALT	M	887	1910	Elevation above sea level in metres
MAP	Mm	750	1529	Mean annual precipitation in mm
MAP20	Mm	864.9	1743.1	Annual precipitation exceeded with 20% frequency (wettest year in 5) in mm
MEDMAP	Mm	744.0	1514.0	Median annual precipitation in mm
MAP80	Mm	611.2	1269.1	Annual precipitation exceeded with 80% frequency (driest year in 5) in mm
JANMEDP...DECMEDP	Mm	0.6	233.9	Monthly median rainfall in mm
MAT	°C	13.8	19.1	Mean annual temperature in °C
JANMINT...DECMINT	°C	1.2	17.2	Monthly mean daily minimum temperatures in °C
JANMAXT...DECMAXT	°C	14.8	27.5	Monthly mean daily maximum temperatures in °C
ANNPEV	Mm	1547.1	1918.5	Annual potential evaporation in mm
JANPEV...DECPEV	Mm	85.1	205.5	Monthly potential evaporation in mm
ANNSRD	MJ.m ⁻² .day ⁻¹	250.9	286.1	Total annual solar radiation in megajoules per square metre per day
JANSRD...DECSRD	MJ.m ⁻² .day ⁻¹	14.0	31.7	Monthly solar radiation in megajoules per square metre per day
SPRMEDP*	Mm	19.8	59.6	Spring median precipitation - sum for months of Aug & Sep.
ESUMEDP*	Mm	253.7	487.7	Early summer median precipitation - sum for months of Oct, Nov, Dec.
WINMEDP*	Mm	3.4	36.7	Winter median precipitation - sum for months of Jun, Jul, Aug.
ESUMINT*	°C	18.2	28.8	Early summer daily mean minimum temperatures - sum for months of Oct & Nov.
SUMMAXT*	°C	85.8	108.7	Summer daily mean maximum temperatures - sum for months of Dec, Jan, Feb & Mar.
ESPRPEV*	Mm	357.1	435.7	Winter potential evaporation - sum for months of Jul, Aug & Sep.
WINSRD*	MJ.m ⁻² .day ⁻¹	47.0	56.0	Winter potential evaporation - sum for months of Jul, Aug & Sep.
SUMSRD*	MJ.m ⁻² .day ⁻¹	73.6	90.5	Winter solar radiation - sum for months of Jun, Jul, Aug.
PXT*		1242	2322	The sum of the products of all the Median monthly precipitation and monthly maximum temperatures
SPRPXT*		580	1057	The sum of the products of Median monthly precipitation and monthly maximum temperatures for Aug, Sep. & Oct.
AUGCI*		0.1	0.8	Median precipitation in Aug. / Mean maximum temperature in Aug.
SEPCI*		0.9	1.9	Median precipitation in Sep. / Mean maximum temperature in Sep.
APRCI*		1.8	3.6	Median precipitation in April. / Mean maximum temperature in April.
CI*		49.2	89.9	MAP / MAT
WATER*		71	122	The absolute value of the difference between Octmedp & Octpev.
SI	M	14.0	26.8	Site index at reference age 15 years
SQ		1	5	Site quality class

*Variables constituted after the initial screening process using combinations that showed significant correlations.

**Environmental variables obtained through the ICFR from the work of (Schulze, 1997).

6.3.5.2 Initially, in a first screening process, the Site Index for each test was regressed and correlated individually with all of the environmental factors available (Table 6.3.2). In this process those factors which showed some significant correlation with Site Index were identified (Table 6.3.3). Several other variables were constituted using the results of this initial process. These

latter variables included factors such as spring median precipitation (SPRMEDP), early summer daily minimum temperatures (ESUMMINT) amongst others (Tables 6.3.2 & 6.3.3).

6.3.5.3 After the initial screening process, a range of multiple linear regression models were run to determine combinations of variables that would explain the variation in tree growth. A sample of some of the multiple regressions that explained at least some of the variation are presented in table 6.3.4.

Table 6.3.3: Correlations for the relationships between environmental variables and Site Index.**

Month	MEDP Corr.	PEV Corr.	MINT Corr.	MAXT Corr.	SRD Corr.
Jan.	-0.16	-0.03	0.00	0.19	0.30
Feb.	0.01	-0.10	0.04	0.20	0.30
March	0.05	-0.14	0.00	0.14	0.17
April	0.04	-0.28	-0.02	0.12	-0.05
May	0.11	-0.31	0.04	0.10	-0.32
June	-0.04	-0.22	0.08	0.11	-0.34
July	0.20	-0.34	0.04	0.09	-0.34
Aug.	0.28	-0.44	-0.01	0.05	-0.29
Sept.	0.11	-0.34	-0.07	-0.05	-0.25
Oct.	-0.24	-0.23	-0.12	-0.01	0.14
Nov.	-0.28	-0.17	-0.11	0.08	0.30
Dec.	-0.16	-0.10	-0.06	0.16	0.31
Annual	-0.08	-0.26	0.05	*	0.10
Seasonal	0.20	ESPRPEV -0.39	*	*	*
	-0.23	*	-0.12	0.17	0.31
	0.21	*	*	*	-0.33
Other	WATER -0.14	SPRPXT -0.01	AUGCI 0.29	SEPCI 0.14	APRCI 0.02
	LAT 0.35	LONG -0.29	ALT -0.21	*	*

*Selected variables which constitute combinations of the primary variables

**Shading refers to correlations significant at the 5% level.

Table 6.3.4: A sample of some of the multiple linear regression combinations of environmental variables tested to look for the combinations that would best explain the differences in Site Index of the 59 test sites.

Variables tested	R ²	Pr > F
FEBMAXT JANMEDP AUGCI WINMEDP*	0.12	0.127
LAT ESPRPEV ESUMEDP	0.17	0.018
LAT AUGPEV ESUMEDP DECSR	0.24	0.005
AUGPEV ESUMEDP DECSR AUGCI	0.24	0.005
LAT AUGPEV DECSR AUGCI	0.28	0.001
LAT AUGPEV DECSR AUGMEDP	0.28	0.001
LAT ESUMEDP WINMEDP AUGPEV	0.31	0.0005

*Tested with other data from commercial compartments and yielding an R² of 0.69 (Pallett, 2001).

6.3.5.4 Several of the environmental variables tested showed some weak relationships with Site index at base age 15 years (Table 6.3.3). The highest correlation with Site Index was a negative

one with August potential evaporation (AUGPEV) as well as other months around that spring period (SEPPEV, ESPRPEV). The correlation of Site Index with AUGPEV was -0.44 and the regression explained 19% of the variation. Other significant correlations were, a negative one with Winter solar radiation (JULSRD), a positive one with summer solar radiation (SUMSRD, DECSR, JANSRD, SUMSRD) a negative one with median monthly precipitation in the spring months (AUGMEDP, OCTOMEDP), a positive one with Spring climate index (AUGCI, SEPCI) and a positive one with latitude (LAT).

6.3.5.5 Some of the multiple linear regressions attempted also explained a small proportion of the variation in Site Index (Table 6.3.4). The initial simple linear regressions identified many of the variables that showed some relationship with Site Index. These were then used in a large range of multiple regressions. The highest coefficient of variation for any of the regressions attempted was 0.31. The variables included in this latter regression were latitude (LAT), early summer median precipitation (ESUMMEDP), Winter median precipitation (WINMEDP) and August potential evaporation (AUGPEV).

6.3.6 Discussion

6.3.6.1 A large range of environmental variables were screened and amongst these considerable differences were found in their relationship with Site Index at base age 15 (Site Index). However, overall, the amount of variation explained by any or a combination of these variables was fairly small. This was surprising, as many previous site factor studies within the region had shown much higher coefficients of determination (R^2). In addition these studies looked at plots in plantations, often with unknown genetics, whereas in the current study genetic structure was in part controlled and the trees were designed experiments where there would be more control of environmental variation. The highest R^2 for any regression in this study was only 0.31. By comparison, many of the other studies with *P. patula* in the region have generally demonstrated much higher levels of correspondence between site factors and some index of tree growth. The latter studies reported R^2 's of 0.84 in the Usutu Forest, Swaziland (Evans, 1974), 0.46 in the Glengarry district of KZN (Grey, 1979), 0.86 and 0.74 in the escarpment area of Mpumalanga respectively (Schutz, 1990), (Louw, 1995).

6.3.6.2 There could be several possible reasons for this. One obvious difference between this study and the others referred to is that the latter studies were all restricted to relatively small geographic areas whereas this study encompassed a large range of *P. patula* in South Africa and Swaziland. The correspondence between Site Index and site factors generally decreases with increasingly larger geographic sampling area (Louw, 1999). However, in an unpublished study

Pallett (2001), showed a R^2 of 0.69 using some of the variables utilized in this study over a similarly wide geographical area.

6.3.6.3 Several other problems associated with this study may have also contributed to the relatively low R^2 s. All the assessments utilized in determining the Site Index were 10 years or younger. Ideally, trees at 15 years of age should be assessed to determine the Site Index at base age 15. The young assessment ages will contribute to poorer precision in the estimates of the Site Index (von Gadow and Bredenkamp, 1992). Trees at a young age will also be affected more by differing silvicultural practices such as weeding and site preparation than an older stand where intraspecific competition is likely to become more important (Oliver and Larson, 1990). Younger trees are also more likely to be affected by silvicultural practices such as weed control (Minogue et al., 1991). *P. patula* tree growth has been shown to be affected by weed competition (Christie, 1994), (Rolando and Little, 2000) and different levels of weed growth could affect estimations of Site Index significantly. In addition, the Site Index estimates were derived from trees dispersed in single line plots replicated across the test. These line plots may be affected by competition from other neighboring genotypes, although this will be ameliorated considerably by randomization and replication. Finally, for some estimates, fewer than the recommended 30 sample trees (Bredenkamp, 1993) were available. All of these problems indicate that the estimates of Site Index could be subject to considerable error.

6.3.6.4 The Site Index was assessed using a number of trees from a small number of genotypes. These could in themselves be subjected to GxE. Indeed, in a number of the trial series the South African genetic checks utilized for the estimation of Site Index were demonstrating considerably high levels of GxE (see chapter 5). This would introduce more error in the estimation of Site Index.

6.3.6.5 Nevertheless, despite the problems listed, several environmental factors were identified as being important in predicting some of the variation in Site Index. The study was focused on the actual tests and sites that are being considered in the broader GxE study. It seems likely that factors identified as having an impact on Site Index would also have an impact on the genotype x environment interaction.

6.3.6.6 Transpiration and Photosynthesis are key processes directly impacted by water availability issues (Kozlowski and Pallardy, 1996) and in South Africa this has been identified as a key constraint for tree growth (Poynton, 1966), (Roberts, 1994). In this study, many of the variables that showed some relationship with Site Index were associated with water availability. Variables such as precipitation, potential evaporation, monthly maximum temperatures, solar

radiation and climate index may, at least in part, be having an effect on water availability for the trees.

6.3.6.7 Perhaps more importantly, many factors highlighted specific seasons where water related issues could be constraining or impacting tree growth (Table 7.3.3 & 7.3.4). A good example of this are those variables associated with spring. Many variables correlated with Site Index were pointing to precipitation and evaporative demand during the early growing season. In particular, variables such as monthly median precipitation (AUGMEDP, OCTMEDP, SRPMEDP) and those associated with evaporative demand (AUGPEV, SEPPEV) were identified as important. At this time of the year early growth may be constrained by a lack of available water after the winter dry season. In contrast, there was little relationship between any of the autumn season variables and growth. For example, compare the climate index for April (APRCI) with the August climate index (AUGCI). The correlation with Site Index in the former was 0.01 and in the latter 0.29. In the months of April and May the soil water deficit is likely to be low and water availability less of a problem. Hence, during this season water may be less of a limiting factor.

6.3.6.8 Another interesting set of variables that related to tree growth was the effect of solar radiation. During the dry winter season when water is limiting and little cloud cover is present, the correlation of solar radiation with tree growth was negative (JUNSRD, JULSRD). During this time trees are likely to be approaching a water deficit and transpiration demands are likely to be detrimental to tree growth. On the other hand, a positive correlation was found between solar radiation and tree growth during the warmer and wetter summer months (DECRSRD, JANSRD). In this latter case, it may be that high cloud cover / rainfall may limit the amount of solar radiation available for photosynthesis.

6.4 The use of type B genetic correlation estimates to group environments

6.4.1 Introduction

6.4.1.1 In this study paired-site analysis has been utilized to estimate Type B genetic correlations for a large number of sites. These Type B genetic correlations provide a measure of genetic correlation between the same trait expressed on two different sites (Burdon, 1977). These estimates enable questions to be directed at the role of the environments in generating interactions. In this section these Type B genetic correlations are used as a tool to try to investigate the range of variation present within the environments sampled and attempt to isolate any predictable variation. This could then be used to develop models for predicting the likelihood of future interactions.

6.4.2 Regression of Type B genetic correlations on the absolute differences between environmental variables.

6.4.2.1 The estimate of Type B genetic correlations involves a paired site comprising two sites with contrasting environmental conditions. As a first screening method the Type B genetic correlations estimates were regressed onto the absolute environmental differences between these 2 sites. This was done for all possible environmental variables available. In this way it was hoped that any obvious relationships between interactions and any environmental factors could be identified. The following criteria were set for the use of any Type B genetic correlations:-

1. Only pairs where both sites had single site heritabilities greater than 0.05 were used.
2. The Type B genetic correlation estimates for volume per tree at 5 years were used as a standard. In some cases this assessment age was not available and in these situations the closest age to 5 years was utilized (Table 6.4.1 & details in Appendix 1).
3. Each pair of sites should have more than 15 common open-pollinated families in both tests.
4. The Type B genetic correlations were calculated using standardized data, to remove any effect caused by heterogeneous variances.

Table 6.4.1: Details of ages and numbers of paired sites, tests and sites utilized in the studies with Type B genetic correlations estimates.

Age	Nr. of pairs	Nr. tests	Nr. of sites	Reasons for age other than 5
3	1	2	2	CAMCORE s15 tests only assessed at 3
4	6	4	2	Sappi S2 series tests 4 years old
5	72	36	14	CAMCORE / Sappi tests
5	21	7	7	Mondi 2 nd gen. OP progeny tests**
6	10	5	5	ICFR tests only assessed at 6 years
8	33	21	7	CAMCORE s1,2,5,6 with Mondi 'extra' tests (8years)
7/8	6	9	5	CSIR 1 st gen. OP Progeny tests**
4/5	10	7	5	Sappi S1(5 years) & S2(4 years) tests
Tot.	158	91*	47*	

*Totals don't add up because certain tests on same sites and other tests used at both 5 and 8.

**Type B genetic correlation estimates supplied by Mondi and CSIR – see appendix 11 & 12

6.4.2.2 A number of additional Type B genetic correlation estimates were supplied by two South African organizations (Mondi and CSIR). These Type B genetic correlations were also derived in the same way as those outlined in chapters 4 and 5. The estimates were incorporated into the data set already derived from the tests in this study and included 12 more sites and 27 separate Type B genetic correlation estimates. The details provided to the author are outlined in Appendix 9 & 10.

6.4.2.3 The relationships between the Type B genetic correlations and these environmental differences were described in a similar way to those in the site factor study in 6.3.3. Each Type B genetic correlation estimate was correlated and regressed individually and in combination with other variables. The results of some of these are presented in Table 6.4.2. The same descriptors were utilized as in the site factor study (Table 6.3.2).

Table 6.4.2: Correlations for the relationships between the absolute differences between environmental variables and Type B genetic correlations.**

Month	MEDP Corr.	PEV Corr.	MINT Corr.	MAXT Corr.	SRD Corr.
Jan.	-0.14	-0.09	-0.13	-0.04	-0.07
Feb.	-0.06	-0.15	-0.12	-0.03	-0.06
March	0.00	-0.14	-0.15	-0.08	0.00
April	-0.10	-0.14	-0.15	-0.11	-0.03
May	-0.04	-0.14	-0.11	-0.14	-0.04
June	-0.07	-0.16	-0.08	-0.13	-0.05
July	-0.05	-0.14	-0.10	-0.14	-0.04
Aug.	0.04	-0.07	-0.14	-0.15	-0.03
Sept.	-0.05	-0.12	-0.16	-0.14	-0.04
Oct.	-0.23	-0.15	-0.17	-0.12	-0.01
Nov.	-0.13	-0.09	-0.17	-0.11	-0.07
Dec.	-0.17	-0.06	-0.16	-0.05	-0.09
Annual	-0.13	-0.15	-0.14	*	0.01
Seasonal	SPRMEDP 0.02	ESPRPEV -0.11	*	*	*
	ESUMMEDP -0.18	*	ESUMINT -0.17	SUMMAXT -0.05	
	WINMEDP 0.00	*	*	*	WINSRD -0.04
Other	WATER -0.08	SPRPXT -0.19	AUGCI 0.04	SEPCI -0.01	APRCI -0.04
	LAT -0.11	LONG -0.14	ALT -0.07	MAP20 -0.14	*

*Selected variables which constitute combinations of the primary variables

**Shading refers to correlations significant at the 5% level.

6.4.2.4 None of the environmental factors examined showed a strong relationship with the Type B genetic correlations. Many of those that were weakly correlated also showed similar relationships with growth as measured by Site Index (Table 6.3.3 & 6.4.2). Some examples of this were Annual potential evaporation (ANNPEV), October median precipitation (OCTMEDP) and early summer median precipitation. The highest correlations were found for October median rainfall (OCTMEDP) and a combination of spring rainfall and maximum temperature (SPRPXT). The correlation with Type B genetic correlations in these 2 cases was 0.23 and 0.19 respectively (Table 6.4.2).

6.4.2.5 In addition to simple linear regressions a range of multiple regressions were also modeled, including those that gave a small response with Site Index in the site factor study (7.3.3). None of these showed any dramatic improvement with coefficients of determination never greater than 0.1.

6.4.3 Testing the Type B genetic correlations using an ANOVA approach

6.4.3.1 In addition to the above method, the type B genetic correlation estimates were also utilized to test the importance of selected environmental variables using an ANOVA approach. In using the previous regression method it is assumed that the GxE responds in a linear fashion to the absolute differences amongst variables. This is unlikely to always be the case. A good example is the growth response of *Eucalyptus grandis* to rainfall in South Africa. In an unpublished site factor study with the latter species, 78% of the variation in SI in a subgroup of sites with mean annual precipitation greater than 900mm was explained by a range of climatic and soil variables (Bouwer, 1999). By contrast, looking at those sites receiving less than 900mm of annual rainfall, only 42% of the variation could be explained. It could be hypothesized that under higher rainfall situations, other variables beside water become more limiting whereas below 900mm, water, becomes more important. These sorts of complex interactions amongst environmental factors may be playing a role in determining the GxE in *P. patula* in the region. For this reason, in an attempt to search for suitable, predictable models, another method of examining GxE using discrete groupings was thought to be useful.

6.4.3.2 Initially, in each case the 'environment' defined, was grouped into three categories (Table 6.4.3), and each Type B genetic correlation, representing a measure of the 'similarity' or otherwise, between two sites, as measured by the behavior of similar genotypes on both sites was used as an individual observation. Each Type B genetic correlation was thus grouped into sites defined as 'similar' and those defined as 'different'. The degree in which the correlations concurred with the artificially defined environmental parameter groupings was then assessed using an analysis of variance approach where the environmental categories were regarded as fixed effects in the model.

Table 6.4.3: Selected environmental variables utilized to test the similarity of pairs of sites. Each 'environmental parameter' was categorized into three classes as defined below.

Environmental parameter	Key	Major categories
Latitude	LAT	L < 27°S; M = 27- 30°S; H > 30°S
Water	WATER	L < 80mm; M = 80 – 100mm; H > 100mm
Median Annual Precipitation	MEDMAP	L < 900mm; M = 900 - 1200mm; H > 1200mm
Median Annual Precipitation (driest yr. in 5)	MEDMAP80	L < 700mm; M = 700 - 900mm; H > 900mm
Mean annual temperature	MAT	L < 15°C; M = 15-16.8°C; H > 16.8°C
October median monthly rainfall	OCTMEDP	L < 75mm; M = 75 – 80mm; H > 80mm
September median monthly rainfall	SEPMEDP	L < 30mm; M = 30 – 38mm; H > 38mm
October mean monthly minimum temperature	OCTMINT	L < 9°C; M = 9 - 11°C; H > 11°C
November mean monthly minimum temperature	NOVMINT	L < 11°C; M = 11 – 13°C; H > 13°C
June mean monthly maximum temperature	JUNMAXT	L < 16.5°C; M = 16.5 - 19°C; H > 19°C
July mean monthly maximum temperature	JULMAXT	L < 17°C; M = 17 – 19°C; H > 19°C
May potential evaporation	MAYPEV	L < 100mm; M = 100 – 125mm; H > 125mm
July potential evaporation	JULPEV	L < 95mm; M = 95 – 110mm; H > 110mm
September potential evaporation	SEPPEV	L < 145mm; M = 145 – 160mm; H > 160mm
Spring sum of products of rainfall & max. Temp. for Aug, Sep, Oct	SPRPXT	L < 800; M = 800 – 950; H > 950
September Climate index (Mnth rainfall/ max. temp.)	SEPCI	L < 1.3; M = 1.3 - 1.6; H > 1.6
Early spring potential evaporation (Jul, Aug, Sep)	ESPRPEV	L < 415mm; M = 415 - 430mm; H > 430mm
Early summer median precipitation	ESUMMEDP	L < 265mm; M = 265-350mm; H > 350mm
Early summer Monthly mean minimum temperatures	ESUMMINT	L < 21.5°C; M = 21.5-24°C; H > 24°C
Spring median precipitation (Aug & Sep.)	SPRMEDP	L < 40mm; M = 40 – 50mm; H > 50mm
Annual potential evaporation	ANNPEV	L < 1620mm; M = 1620 - 1840mm; H > 1840mm

6.4.3.3 A number of different environmental factors were tested in this way (Table 6.4.3). These were selected based on the results of the previous site factor and regression studies (see section 6.3 and 6.4.3). This initial investigation gave some indication of potential variables.

6.4.3.4 The results suggested that generally significant differences between classes seemed to be concentrated around those variables associated with describing conditions during the spring season. A few of those utilized further are presented in table 6.4.5. This is the period around the months of August, September and October. Many of these variables are associated with estimating the water availability for the trees at this time of the year (ESUMMEDP & OCTMEDP). This seemed to confirm the general trends found in the earlier Site factor studies.

6.4.3.5 In a second phase of the study a number of different combinations of some of the above variables that showed potential were examined. For these latter investigations many different combinations of various variables were attempted. The boundaries of the classes were also manipulated although consideration was given to the distribution of the sites and in most cases some groupings were apparent. Furthermore, in considering pairs of variables some thought was given to how these were related and whether combining them would be biologically meaningful.

Two of the better combinations of pairs of variables that were attempted are included here and the results of these are presented (Table 6.4.6).

6.4.3.6 The 4 variables utilized were associated in 2 models, where in each model two variable combinations were used. It was found that using more than 2 classes for each variable made the models too complex and unwieldy, and in addition, the number of data points became limiting in that the numbers were too few to allow reasonable estimation of each class contrast.

6.4.3.7 Some detail of the methodology utilized to derive the 2 models (Table 6.4.6), are outlined in table 6.4.4. In each case the first variable listed in the table was utilized for the first division into 2 classes, followed by a further division using the second variable to obtain 4 defined regions. As an example for Model 1, these 4 regions were classified as follows:-

A = High OCTMEDP & High JUNPEV

B = High OCTMEDP & low JUNPEV

C = Low OCTMEDP & High JUNPEV

D = Low OCTMEDP & Low JUNPEV.

In each case the first variable cited is the one utilized to make the first broad division. Any pair of sites would thus be a contrast between or within these 4 regions and this equates to a maximum of 10 classes, ranging from AA, BB, CC & DD as pairs within regions to AB, AC, AD, BC, BD & CD as pairs across regions (Table 6.4.6).

Table 6.4.4: Details of the variables and definition of class boundaries utilized for the construction of the three 2-variable models

Model	Variables	Class boundaries defined
Model 1 (OCTMEDP & JUNPEV) (OPJV)	OCTMEDP* JUNPEV	Min. = 56.1; LOW < 75 < HIGH; Max. = 91.4 Min. = 85; LOW < 99 < HIGH; Max. = 108.3
Model 2 (ESUMMEDP & JULMAXT) (ESPJX)	ESUMMEDP* JULMAXT	Min. = 232; LOW < 414 < HIGH; Max. = 455 Min. = 15; LOW < 18 < HIGH; Max. = 21.5

*Variable used to make the first division between classes

Table 6.4.5: The number of pairs, Type B genetic correlation means, minima, maxima and empirical standard errors in each class for 4 selected environmental variables tested using the ANOVA approach and showing significant differences between classes.

Variable	Class	Nr.	Mean	Min.	Max.	Stderr	Prob>F*
OCTMEDP (OP)	HH	51	0.78	0.20	1.00	0.032	0.019
	HL	85	0.66	0.00	1.00	0.026	
	LL	22	0.76	0.35	1.00	0.043	
JUNPEV (JV)	HH	19	0.82	0.24	1.00	0.044	0.026
	HL	86	0.67	0.00	1.00	0.027	
	LL	53	0.74	0.20	1.00	0.031	
JULMAXT (JX)	HH	42	0.78	0.00	1.00	0.035	0.07
	HL	87	0.68	0.10	1.00	0.025	
	LL	29	0.74	0.15	1.00	0.048	
ESUMMEDP (ESP)	HH	8	0.88	0.59	1.00	0.054	0.064
	HL	63	0.68	0.00	1.00	0.031	
	LL	87	0.72	0.15	1.00	0.025	

*Fprob from an ANOVA testing for significant differences between each class for each environmental variable.

Table 6.4.6: The number of pairs, Type B genetic correlation means, minima, maxima and empirical standard errors in each class for two selected 2-variable models tested using the ANOVA approach and showing significant differences between classes.

Variable	Class	Nr.	Mean	Min.	Max.	Stderr	Prob>F*
Model 1 (OP-JV)	AA	10	0.87	0.59	1.00	0.044	0.022
	AB	32	0.73	0.23	1.00	0.042	
	AC	7	0.75	0.24	1.00	0.095	
	AD	34	0.62	0.00	1.00	0.042	
	BB	9	0.82	0.20	1.00	0.085	
	BC	12	0.55	0.15	0.93	0.067	
	BD	32	0.73	0.21	1.00	0.040	
	CC	2	0.82	0.70	0.94	0.118	
	CD	8	0.82	0.35	1.00	0.073	
	DD	12	0.71	0.38	1.00	0.060	
Model 2 (ESP-JX)	AA	8	0.88	0.59	1.00	0.054	0.098
	AC	22	0.70	0.00	1.00	0.055	
	AD	37	0.65	0.10	1.00	0.040	
	BC	1	0.96	0.96	0.96		
	BD	3	0.74	0.45	1.00	0.159	
	CC	12	0.84	0.50	1.00	0.051	
	CD	49	0.69	0.20	1.00	0.031	
	DD	26	0.74	0.15	1.00	0.052	

*Fprob from an ANOVA testing for significant differences between each class for each environmental variable.

6.4.3.8 All of the models presented here gave some indication of the potential to differentiate between classes and particularly demonstrated differences between the Type B genetic correlation estimates within and between regions. The highest differentiation, when simply contrasting like and unlike groups, was for model 1 and gave a difference of 0.11.

6.4.3.9 The same level of differentiation was found when using some of the variables in isolation. These included OCTMEDP, JUNPEV and ESUMMEDP. In each of these three cases a

differentiation of around 0.11 – 0.12 was achieved. A map of the two potential regions using October median monthly rainfall for the *P. patula* areas in Southern Africa illustrates how such a regionalisation scheme might partition the land base (Figure 6.4.1).

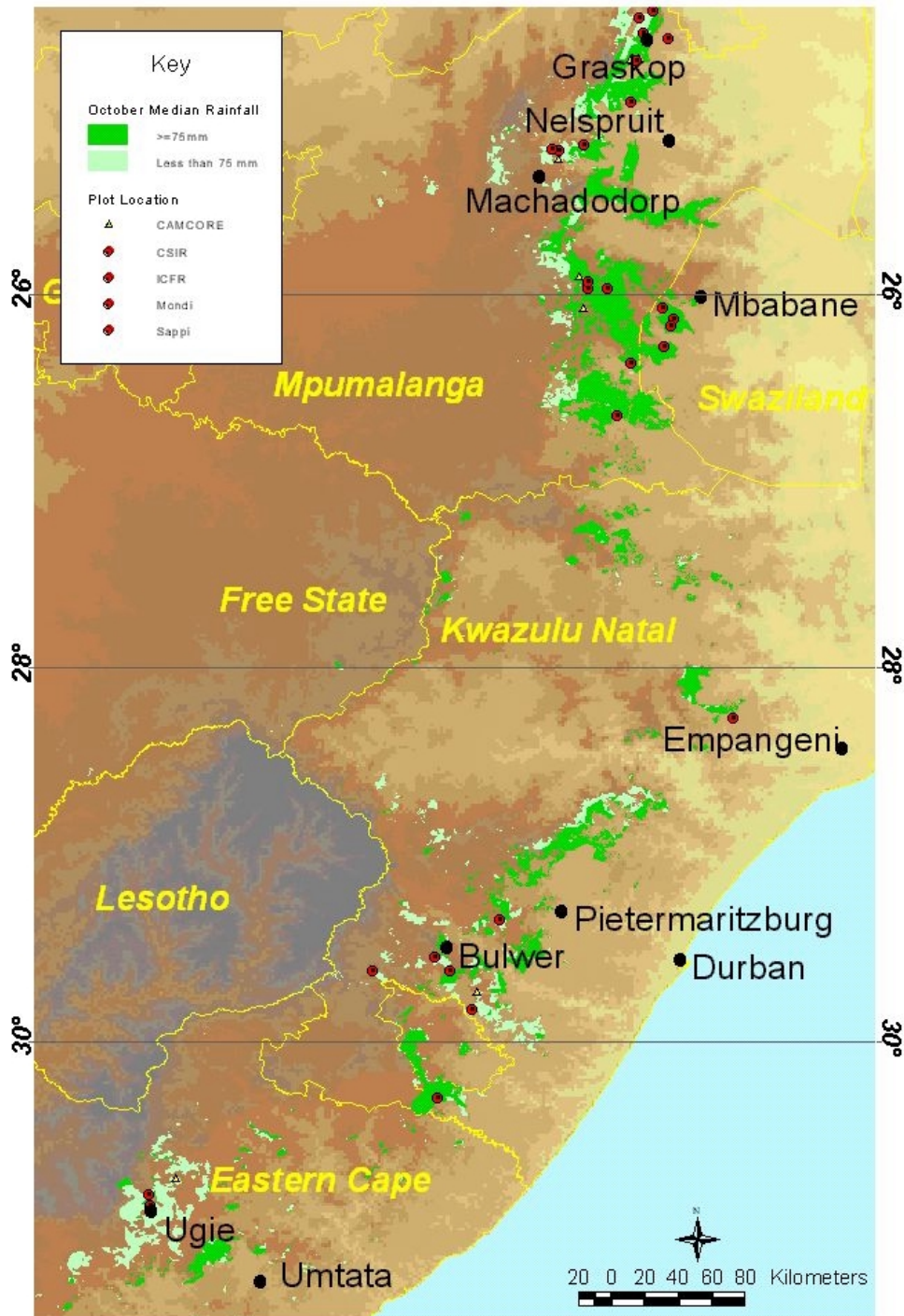


Figure 6.4.1: Map of the *P. patula* areas in Southern African (South Africa and Swaziland) with an indication of the regionalisation as defined by October median monthly precipitation.

6.4.4 Discussion

6.4.4.1 The GxE utilized in this section has been quantified as the genetic correlation between pairs of sites (Type B genetic correlations) over 158 pairs in 91 tests over 47 sites (Table 6.4.1). These Type B genetic correlations give a useful indication of the extent of the 'similarity' between pairs of sites and puts the emphasis on the environments rather than the genotypes. The precision of these estimates is, however, low and a large number of tests are needed to attempt to identify predictable GxE (Hodge, 1996). This can be clearly seen when considering the minimum and maximum Type B genetic correlations for all classes (Table 6.4.5 & 6.4.6). In all cases, regardless of class and the means of those classes, most of the contrasts tested had maximum Type B genetic correlations close to 1.00 and in some cases they varied from 0 – 1.00. Thus, the particular paired-site estimates generally are associated with high empirical standard errors.

6.4.4.2 Many of the environmental variables that were identified as having some relationship with site index also demonstrated some correlation with GxE as measured by the Type B genetic correlations (Table 6.3.3 & 6.4.2). In particular, variables associated with water availability (rainfall and evaporative demand) were found to correlate best with both tree growth and the measure of GxE for volume. This should not be entirely surprising as those factors constraining growth may also be those that allow certain 'better' adapted genotypes to compete more effectively under certain growth limiting conditions.

6.4.4.3 The second approach in utilizing the Type B genetic correlations was to group the environmental variables into classes and then test classes of 'like' and 'unlike' pairs using an ANOVA method. This narrowed down the list of potential candidates even further and again highlighted the apparent critical importance of the spring season. Mean median precipitation during the spring months (OCTMEDP & ESUMMEDP) were selected amongst the 4 remaining variables. The other two variables selected were evaporative demand in winter (JUNPEV) and mean maximum monthly temperatures in July (JULMAXT). These two latter variables describe the conditions over the winter period and will also be associated with water availability. The maximum temperature variables during winter may also be important in defining the level of active growth and extent of dormancy that sites will impose on the trees.

6.4.4.4 The above variables also differentiated between those classes comparing 'same' sites to those with 'different' sites reasonably effectively. This gives some indication of predictable GxE. As an example consider the OCTMEDP results; The 'HH', and 'LL' classes, representing those pairs where both sites have high or low median monthly rainfall respectively, had mean Type B genetic correlations of 0.78 and 0.76 respectively (Table 6.4.5). In contrast, the 'HL' class had a mean Type B genetic correlation of 0.66 respectively. In other words, the correlations were higher in both 'like' classes than the 'unlike' comparison. Indeed the mean for the 'unlike' class had a Type B genetic correlation below 0.67, while those from both 'like' classes had levels well above this. This level, which equates to a situation where the GxE variance is half the size of the additive genetic variance, has often been cited as a critical level. In this case it also is close to the average Type B genetic correlation estimate for the entire land base. A GxE greater than this, in other words a Type B genetic correlation < 0.67 , has been quoted as having potentially serious implications for gains from selection (Shelbourne, 1972).

6.4.4.5 The example using OCTMEDP is duplicated to a greater or lesser extent in all of the other variables tested (Table 6.4.5). In each case, both comparisons of 'like' classes always have higher estimates of average Type B genetic correlations than the 'unlike' classes.

6.4.4.6 The results also suggest that the GxE is not driven by one variable but is likely to be influenced by a complex range of variables affecting the growth of individual genotypes in many different ways. It would thus be reasonable to try combinations of variables in an attempt to find better explanatory factors. Many different combinations and classes were attempted.

6.4.4.7 A number of limitations were associated with attempting to define multivariate models. The estimated Type B genetic correlations available placed restrictions on the number of classes and regions that could be tested. It was desirable to include at least 10 to 15 estimates in any one class because the standard errors for any mean estimates with fewer points tended to be very high. Incorporating more variables increased the complexity and numbers of classes and regions rapidly so that on a practical level only two-variable models were attempted. In addition, consideration needed to be given to the phenotypic correlations between variables and this limited the number of combinations that could be attempted. Many of the variables were related and correlated and indeed in many cases some were not independently derived. These latter considerations also restricted the combinations that could be attempted.

6.4.4.8 The four two-factor models presented (Table 6.4.6) all differentiate between classes and indicate that these differences are statistically significant. In most cases the pairs within regions had higher Type B genetic correlation estimates than between regions. In addition, the 'unlike'

comparisons were in many cases substantially lower than in corresponding 'like' classes. However, these significant differences between classes did not always differentiate between pairs within region from those across regions. In some cases the 'like' classes had lower Type B genetic correlation estimates than 'unlike' classes. This latter problem may in part be due to poor estimation of class means due to inadequate numbers of data points per class mean. In addition, a comparison of 'like' and 'unlike' classes, using a two-variable model, does not in fact achieve a better differentiation than just using single variables. The two-variable models may however provide a greater degree of differentiation between certain classes. The spread in estimates in model 1 for example, ranges from 0.55 to 0.87.

6.4.4.9 All of the above results suggest that there may be sufficient grounds for saying that some predictable GxE is apparent. Furthermore, given all of the constraints and imprecision associated with the estimations of the Type B genetic correlations, the identification of the spring season, and perhaps to a lesser extent winter descriptors as key indicators should not be ignored. An attempt to develop any regionalisation model should take cognizance of these results.

6.5 Towards a tentative GxE regionalisation model

6.5.1 Introduction

The previous sections have examined a range of variables and isolated a small number that may be relevant in attempting to identify the patterns of GxE in a predictable manner. It remains important to look a little more critically at these variables and try to determine to what extent these statistical indications are geographically and biologically meaningful. An attempt will be made to examine these issues, and in the context of the data available, propose a regionalisation model or models.

6.5.2 A critical look at some of the identified environmental variables

6.5.2.1 There is a need to look a little more closely at the variables that do offer some potential in predicting GxE in the region. A possible option, already considered, could be to combine 2 or more variables in trying to derive an effective model. However, the relationship amongst the variables needs to be considered and in addition, how they were derived. It is highly likely that factors such as rainfall, potential evaporation and the amount of solar radiation available will be correlated and the issue of multicollinearity should not be ignored.

6.5.2.2 The extent of correlation amongst the variables (multicollinearity) was examined for a range of potential variables. The correlation between each and every variable was examined and those during the critical spring period are presented in table 6.5.1.

Table 6.5.1: Correlations between environmental variables that have been identified as having some potential for predicting GxE.

Variable	JUN-PEV	JUN-MEDP	JUN-MAXT	JUL-MAXT	AUG-PEV	AUG-MEDP	AUG-MAXT	OCT-PEV	OCT-MEDP	OCT-MAXT	ESUM-MEDP
MEAN	95.9	3.6	17.7	18.0	140.2	8.9	20.1	172.9	73.5	22.8	348.0
STD	8.1	2.1	1.7	1.7	11.1	5.3	1.5	18.5	8.4	1.5	64.4
Nr.	59.0	59.0	59.0	59.0	59.0	59.0	59.0	59.0	59.0	59.0	59.0
JUNPEV	1.00	0.32	0.44	0.46	0.71	-0.14	0.55	0.94	0.42	0.61	0.74
JUNMEDP	0.32	1.00	0.52	0.53	-0.12	0.51	0.53	0.31	0.30	0.60	0.49
JUNMAXT	0.44	0.52	1.00	1.00	-0.10	0.68	0.98	0.43	0.39	0.93	0.42
JULMAXT	0.46	0.53	1.00	1.00	-0.06	0.65	0.99	0.46	0.42	0.94	0.46
AUGPEV	0.71	-0.12	-0.10	-0.06	1.00	-0.70	0.06	0.76	0.46	0.15	0.65
AUGMEDP	-0.14	0.51	0.68	0.65	-0.70	1.00	0.54	-0.26	0.07	0.43	-0.04
AUGMAXT	0.55	0.53	0.98	0.99	0.06	0.54	1.00	0.57	0.45	0.98	0.52
OCTPEV	0.94	0.31	0.43	0.46	0.76	-0.26	0.57	1.00	0.47	0.67	0.76
OCTMEDP	0.42	0.30	0.39	0.42	0.46	0.07	0.45	0.47	1.00	0.45	0.86
OCTMAXT	0.61	0.60	0.93	0.94	0.15	0.43	0.98	0.67	0.45	1.00	0.58
ESUMMEDP	0.74	0.49	0.42	0.46	0.65	-0.04	0.52	0.76	0.86	0.58	1.00

6.5.2.3 As expected, several of the environmental variables were correlated with each other (Table 6.5.1). In many instances variables that were utilized were correlated, such as mean monthly precipitation in October (OCTMEDP) and mean potential evaporation in June (JUNPEV). The median monthly rainfall figures were generally correlated with potential evaporation and maximum temperatures in most months. This is to be expected as these variables are associated and not independently estimated. However, in several situations, variables were derived from other variables and this needs to be carefully considered.

6.5.2.4 All of the variables utilized in this study are derived using models from a network of climatic stations. The basis for the climatic parameter mapping was a 1 minute by 1 minute grid covering the entire region (Schulze, 1997). The models were developed using physiographic, locational and climatic attributes and statistical techniques such as stepwise multiple regression methods. Checks were then built in to test whether or not values were physically realistic at those locations. In this way estimates of all the variables utilized were derived for all locations in the region. For the purposes of this study it was important to consider to what extent certain variables were derived from other ones (Table 6.5.2).

Table 6.5.2: The nature of the derivations for the variables identified as having some potential to predict GxE.

Variable	Derivation*
Median precipitation	Independently, derived using rainfall figures from weather stations with other input variables such as altitude, distance from sea, aspect amongst others.
Maximum temperatures	Derived from weather stations and interpolated using factors such as latitude, altitude, longitude amongst others.
Solar radiation	Derived from extraterrestrial solar radiation, daily maximum air temperatures and daily temperature range
Potential evaporation	Derived from A-pan equivalent reference evaporation estimates as well as interpolated from monthly mean daily maximum temperatures, extra-terrestrial solar radiation for month, median monthly precipitation.

*Information obtained from (Schulze, 1997).

6.5.2.5 A consideration of the derivation of the variables identified reveals that essentially the precipitation and temperature variables were independently derived. The solar radiation and potential evaporation estimates were, in part derived using temperature and / or rainfall data. The use of the latter 2 variables in conjunction with monthly maximum temperature and rainfall data would thus need to be carefully considered.

6.5.2.6 Several permutations for each of the variables under consideration were tested. It could be considered reasonable to test these variables in some form of multiple regression. Multiple regressions have been tried using the absolute differences between the environmental parameters for pairs of sites (see section 6.4.2.3). These attempts did not prove to be successful with the best model only giving a coefficient of determination of 0.08, when using r_{Bg} 's as the dependent variable.

6.5.2.7 Another approach in trying to utilize a combination of these variables has been attempted by defining groupings of the variables in classes and testing using an ANOVA approach. This approach was able to differentiate some predictable GxE but the actual differences were relatively small. (section 6.4.3).

6.5.3 Discussion and proposal of a GxE model

6.5.3.1 *P. patula* is only planted in the summer rainfall areas of the region. This climate is characterized by a wet rainy season during summer followed by a dry winter. Typically the rainy season occurs from around October through to April, providing conditions associated with good tree growth due to the combination of warm temperatures and a plentiful supply of water. During autumn (April and May), the rainfall drops off and temperatures begin to decrease. However, soil moisture remains high and tree growth continues well into June and even July, depending on the site. The winters (June, July and August) are characterized by cold nights and mild daytime

temperatures. However, during this season little or no rain falls and the soils begin to dry out so that by July and early August little or no growth is occurring. Finally, during spring, the temperatures and rainfall increase from around August through to October. During this latter period as temperatures and day length increases, the trees begin growing rapidly but may be constrained by the available soil moisture. This period may thus be critical and the conditions may vary from site to site depending on the distribution of early rainfall and cloud cover.

6.5.3.2 To better understand the effects of the environmental variation described, it is necessary to consider the growth characteristics of the species in the region. The pattern of annual growth typically involves the production of between 1 and 5 internodes (Evans, 1978). Current annual height increment increases to a maximum in about the fourth year and this is paralleled by the number of internodes produced and, more erratically, also by internode length. The number of internodes increases from around 2 per year, averaging around 0.18m in length at 1 year to around 5 nodes averaging 0.41m at 4 years. After this, both the annual internode production and internode length decreases till it may only average one per year in trees of 25 years and older (Norskov-Lauritsen, 1963). The average needle longevity for the species is between 16 months to as long as 4 years (Olbrich, 1993), (Wormald, 1975), with needle senescence occurring mainly from February through into winter (Table 6.5.3).

6.5.3.3 The 'average' phenological stages for *P. patula*, along with two examples of 'typical' rainfall and temperature distributions in Southern Africa, are presented in table 6.5.3. The species is characterized by only a very short dormancy period of around 1 month around July and August (Norskov-Lauritsen, 1963). This is followed by rapid shoot elongation in the early season from August to October and a slower longer phase from November through to May (Olbrich, 1993). A study in the Mpumalanga region on two diverse sites (950m and 1520m elevation) indicated that the rapid spring growth flush started simultaneously in both regions (Payn et al., 1989). This latter finding suggests that light intensity or day length may influence this initial flush.

Table 6.5.3: An example of rainfall and temperature distribution over 12 months for two of the *P. patula* sites along with a summary of the phenological stages* occurring in the species in South Africa.

SITE	Parameter	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	JUL
Helv. E7	MEDP(mm)	1.7	18.1	61.7	118	116	120	97.8	80.1	41	8.4	0.9	0.8
(Alt.=1701m)	Month Min. Temp(°C)	4.7	7.5	9.7	11.2	12.5	13	12.8	11.7	9	5.6	2.8	2.8
20-07-09B	Month Max. Temp(°C)	18.7	21	21.5	22	22.9	23.4	23	22.3	20.5	18.6	16.1	16.4
Tweef. C51	MEDP(mm)	12.8	34.8	79.3	158	180	192	166	139	65.7	21	6.2	8.8
(Alt.=1160m)	Month Min. Temp(°C)	7.4	10.1	12.2	13.9	15.2	15.7	15.6	14.6	12	8.5	5.5	5.4
PG028T	Month Max. Temp(°C)	22.2	24.2	25	25.2	26.1	26.5	26.3	25.6	24.1	22.3	19.8	20.2
Phenological stage	Description	Early season			Mid-season			Late season			Winter		
Node formation	Late season initials formed												
	New initials formed after extension of early nodes												
Shoot extension	Rapid early growth												
	Moderate slower growth												
Winter	Slow growth or dormancy												
Needle extension	Base needles formed - negligible extension												
	Needle elongation												
Needle Senescence	Needles fall off tree												

*From (Olbrich, 1993).

6.5.3.4 The results presented in the previous sections suggest that the period around the spring months (August to October) influence at least a portion of the GxE in the species. It is suggested that a combination of rapid growth stimulated by day length / light intensity and a potential water availability constraint may be contributing to this GxE. Certain genotypes may be more able to exploit (either physiologically or morphologically) the situation that varies by the level of moisture stress in the different environments. Apparently, extending the length of the growing season by flushing earlier is not the mechanism. The study alluded to earlier suggests that trees, presumably from diverse genetic stock, on two diverse sites commenced growth simultaneously in spring (Payn et al., 1989).

6.5.3.5 The conditions during the winter months may also be critical. During this period from June into July, little rain falls and the soils begin to dry out. In addition, temperatures drop and particularly at night, sub zero temperatures and frost may be common. A combination of less water availability and colder temperatures are likely to impose some form of winter dormancy or at least dramatically slower growth during this period. However, this is likely to vary between sites depending on the amount of rainfall, evaporative demand and temperatures, and variation in these may restrict or increase the length of the growing season. The correlations between tree

growth as measured by site index (Table 6.3.3) were higher for mean monthly potential evaporation than temperatures and this may indicate that water, or the lack of it during this period, may be more critical to growth than temperatures. In either case, and especially because these variables are correlated, the months of June and July have also given indications of being critical for GxE, as suggested by the two 2-variable models proposed (Table 6.4.6).

6.5.3.6 In the light of the above discussion several simple models are proposed (Table 6.4.6). These include defining just two regions by single variables such as median monthly precipitation in October (OCTMEDP), total monthly median rainfall for the summer months of October, November and December (ESUMMEDP) or mean potential evaporation in June (JUNPEV) as outlined in table 6.4.5. Alternatively, a combination of rainfall and winter factors such as the models 1 and 2 (Table 6.4.6) could be utilized to define 4 regions.

CHAPTER 7: CONCLUSIONS AND EVALUATION OF THE PRACTICAL APPLICATION OF GxE

Chapter Summary

7.1 Introduction

7.2 Identification of GxE and its quantification

7.3 Identification of the type of interactions and the interacting genotypes and environments.

7.4 The grouping of genotypes and environments to partition GxE

7.5 Determination of potential impact and practical application of GxE

7.1 Introduction

7.1.1 Any study of GxE should include five important objectives when considering this topic (Bridgewater and Stonecypher, 1978). These can be summarized as follows:-

1. Recognize its presence (and quantify the amount)
2. Identify interacting genotypes
3. Identify interacting environments
4. Group genotypes and environments to partition GxE
5. Determine its potential impact

This study has considered the first four objectives and will address the fifth objective in this chapter. The first four objectives will be briefly discussed and summarized in sections 7.2 to 7.4 whilst the final section will consider its potential impact and discuss other practical applications of the study.

7.2 The identification and quantification of GxE

7.2.1 The suspicion that GxE may be important in Southern Africa for *P. patula* has been reported for a number of years (Denison, 1973), (Falkenhagen, 1979), (Barnes et al., 1992), (Snedden and Verry, 1999). However, none of the previous studies, with the exception of the last mentioned one, went any further than reporting its presence. The latter study (Snedden and Verry, 1999), suggested some responses for breeding the species but only really looked at the Mpumalanga region of South Africa.

7.2.2 In this study, the entire region encompassing South Africa and Swaziland was considered. A large number of provenance and progeny tests were available for analysis. The exact number of tests, origin and structure, and sites are summarized in table 7.2.1. The material available encompassed a broad sample of the entire region, utilizing 81 tests on 54 sites. In addition, the tests included representative populations from almost the entire range of the populations in Mexico as well as material originating and selected from the South African land race. The latter tests included both first and second-generation open-pollinated families. It should be noted however, that no single genotype was common to all tests, and indeed each trial series seldom included more than between 5 to 10 tests.

7.2.1: A summary of the tests available in determining GxE in Southern Africa, including details of the number of tests and sites, as well as a brief description of origin.

Origin	Age	Nr. of tests	Nr. of sites	Description
CAMCORE	3-8	43	22	Provenance/progeny tests including collections from a broad sample of the entire range of <i>P. patula</i> in Mexico.
FAO – Oxford	8-10	8	8	Provenance tests including some similar material as CAMCORE collected from Mexico but not including family structure.
ICFR	6	5	5	Open-pollinated 1 st gen. families selected from the South African land race in KZN.
Sappi	4-5	9	7	Open-pollinated 2 nd gen. Families selected from the South African land race in Mpumalanga.
CSIR*	7-8	9	5	Open-pollinated 1 st gen families selected from the South African land race, mainly in Mpumalanga
Mondi*	5	7	7	Open-pollinated 2 nd gen. Families selected from the South African land race – place of selection nor known by author.
		Total 81	54	

*Type B genetic correlation estimates supplied by Mondi and CSIR – no raw data available.

7.2.3 The amount of GxE present overall was quantified and in addition, the material available gave some opportunity for comparing the GxE across different populations and between the Mexican and South African material.

7.2.4 The overall mean Type B genetic correlation estimate for all tests across all sites was 0.62. These estimates were however done without standardization and perhaps a more meaningful estimate should exclude the effects of heterogeneous variances. These latter estimates varied from 0.68 for the mean of the imported CAMCORE material to 0.76 for the South Africa first generation ICFR families to 0.62 for the Sappi 2nd generation families (Table 7.2.2). Overall, therefore, the average Type B genetic correlation estimate was around 0.69 which equates to a GxE variance that is 50% of the genetic variance.

7.2.5 These overall means can however, be very misleading as they mask the variation between populations which may in fact, be far more interesting and revealing than the mean. Amongst the Mexican imported material considerable variation exists. The combined family – provenance Type B genetic correlation estimates varied from 0.61 to 0.72 (Table 7.2.2). Generally the tests that included families representing samples from the northern provenances were more interactive. In addition, for the northern Mexican material it was the provenance effects that were particularly interactive.

Table 7.2.2: Mean Type B genetic and provenance correlations for the major trial series analyzed in this study.

Origin	r_{BG}	r_{BP}	r_{Bg}^*
CAMCORE series 01 – representing provenances from the central part of <i>P. patula</i> 's distribution in Mexico	0.79	0.68	0.75
CAMCORE series 02 – representing provenances from the southern part of <i>P. patula</i> 's distribution in Mexico	0.75	0.80	0.72
CAMCORE series 05 – representing provenances from the northern part of <i>P. patula</i> 's distribution in Mexico	0.76	0.42	0.72
CAMCORE series 06 – representing provenances from the northern part of <i>P. patula</i> 's distribution in Mexico	0.64	0.58	0.61
CAMCORE series 07 – representing provenances from the northern part of <i>P. patula</i> 's distribution in Mexico	0.78	0.55	0.62
Mean of CAMCORE / Mexican imported material	0.74	0.61	0.68
ICFR series – representing 1 st generation selections from South African land race origin in KZN	*	*	0.76
Mondi series – representing 2 nd generation selections from South African land race origin**	*	*	0.71
Sappi series – representing 2 nd generation selections from South African land race origin in Mpumalanga	*	*	0.62
Mean for the South African material	*	*	0.70
Overall mean	*	*	0.69

*The aggregate family-provenance Type B genetic correlation

**Obtained from Mondi – raw data not available

7.2.6 Comparing the amount of GxE for the imported Mexican and South African material, reveals little difference. The CAMCORE average was 0.68 and the South African material 0.70. This is perhaps a little surprising because the expectation would be that the imported Mexican material would be more interactive. Amongst the South African material the Sappi families were most interactive and this may in fact be a reflection of the environments sampled. Considerable differences between the sites in this series exist.

7.3 A discussion of the types of interactions and the identification of interacting genotypes and environments

7.3.1 On the whole, standardizing the data did not have a large effect on the estimation of GxE as measured by the Type B genetic correlations. The exception is generally confined to those test series where potentially large differences in growth exist. This becomes particularly crucial when utilizing tests assessed at different times. Despite the relatively small overall discrepancies, it seems appropriate to standardize data before these analyses to remove any effects caused by heterogeneous variances.

7.3.2 It has been suggested that in some cases the interaction variance can be attributed to just one or two 'interactive' environments. Some previous studies have suggested this (Woolaston et al., 1991),(Carson, 1991). The Type B genetic correlation estimates where interactions can be grouped per test allowed a comparison of these effects. The mean Type B genetic correlations per site do vary from 0.45 to 0.91 for the CAMCORE tests and between 0.43 and 0.91 for the South African material(Table 5.3.1 & 5.3.2). However, in none of the trial series examined can high levels of GxE (i.e. low Type B genetic correlations) be attributed to only 1 or 2 tests or sites. Generally, moderate to high GxE variance between each individual test and the others is apparent in most of the tests.

7.3.3 There are a few exceptions to above, for example the Bulwer test in the ICFR series and the Jessievale test (20-10-01B) in the CAMCORE 01 series had average Type B genetic correlation estimates of 0.91. One possible explanation might be that these tests measured the genetic differences less precisely and would thus mask 'real' Type B genetic correlations. However, in neither of these two cases was the single site heritability the lowest in their respective trial series. In addition, no obvious environmental factor could be attributed to these exceptions.

7.3.4 An examination of the actual genotypes that contribute towards the interaction variance is also critical. Many previous GxE studies have found that the GxE variance can often be attributed to a small proportion of unstable, interactive genotypes (Li and McKeand, 1989), (Dvorak and Ross, 1994) and (Johnson, 1992). This was examined in this study using the joint regression analysis.

7.3.5 The proportion of interactive genotypes differed markedly amongst the range of populations and sites sampled. Amongst the Mexican (CAMCORE) populations the proportion varied from 9 to 40%. The provenances from the southern and central area of the distribution of *P. patula* in Mexico (series 01 & 02) had a relatively smaller proportion of reactive genotypes (10%) whilst the proportion was considerably higher (18 – 40%) amongst the populations represented by the more northern provenances (series 05 – 07). This is in agreement with the findings of the overall level of GxE (see section 7.2). When considering specific provenances, the Conrado Castillo and Pinal de Amoles tended to be more stable with regression coefficients less than 1. Potrero de Monroy and Zacualtipan on the other hand, representing the more central provenances, tended to be more reactive to site quality with regression coefficients greater than 1 at least when compared to the former two populations.

7.3.6 Amongst the South African improved material the proportion of reactive genotypes was around 10 – 16%. Amongst the 1st generation ICFR families the proportion was 10% and for the mainly 2nd generation Sappi tests the proportion was closer to 16%. This again ties up with the findings of the overall GxE levels which were shown to be higher amongst the 2nd generation Sappi material.

7.3.7 The proportion of interactive genotypes identified thus varies from around 10 – 40%. Not all of these genotypes represent the best performing families and several do not exhibit actual rank changes. South African breeders will need to make some critical decisions on how to utilize this information. It may be advantageous in many situations to ignore the unstable families and select good, stable performers for the breeding program. On the other hand, the identification of the northern provenances as relatively better performers on the poorer site qualities may offer some advantages in breeding for the harsher, poorer, more marginal sites in Southern Africa.

7.3.8 Finally, it should also be noted that the range of material available gave some opportunity to compare the differences in response to environments amongst populations. In addition to the differences in the level of GxE, examples of which have already been discussed above, there were some indications that different populations may be responding to a number of environmental variables. If this is the case this would add another level of complexity to the already considerable challenge of identifying important factors in the environment that affect GxE.

7.4 The grouping of genotypes and environments to partition the GxE

7.4.1 The issue of finding predictable GxE by identifying contributory environmental variables is the most challenging and by far the most crucial issue if GxE is to be utilized in any way. 'For genotypes to be matched to environment, those environments need to be well-defined and repeatable' (Matheson and Cotterill, 1990). Indeed, amongst the vast range of publications examining the issue of GxE very few actually identify the causal factors. A few studies have identified regions that partition some of the GxE, but many of these define geographic or political regions rather than factors in the environment per se (Adams et al., 1994), (Hodge and Dvorak, 1999). One study with *P. elliotii* does identify site quality as a contributing factor (Hodge and White, 1992) while others soils (Ronnberg-Wastljung and Gullberg, 1994) or an index of climatic factors (Alia et al., 1997).

7.4.2 In this study a comprehensive range of climatic variables such as rainfall, temperature, potential evaporation and solar radiation were examined. Initially, to get an indication of the sort of variables that effect growth, a site factor study was done using the growth of the trees in the

tests themselves. This study identified variables associated with rainfall and evaporation during the early growing season, in spring as being important, along with those during the critically dry winter months of June and July.

7.4.3 An attempt was then made to try to relate these variables to the variation in GxE using 158 Type B genetic correlations in 91 tests over 47 sites. Initially this was attempted by regressing the absolute differences of environmental variables for pairs of sites with the Type B genetic correlations. This study again identified similar variables to those in the former site factor study although the correlations were very low.

7.4.4 Finally the test (sites) were grouped into classes, based on environmental variables, and the differences in Type B genetic correlation estimates was tested using an Analysis of Variance approach. The variables that had been identified from the previous studies were of primary interest, although all environmental factors were examined. This exercise did lead to the proposal of some tentative models using again factors such as the spring rainfall (median October monthly rainfall) and winter potential evaporation (June potential evaporation). These models were able to differentiate a difference in Type B genetic correlation estimates of 0.11 and should be regarded as 'experimental' or provisional models that will need to be further evaluated in the future.

7.5 The potential impact and practical application of GxE

7.5.1 Introduction

7.5.1.1 Assessing the potential impact and practical application of GxE is probably the most important aspect of any GxE study. It is necessary to assess to what extent the knowledge of GxE, as derived from this work, can have an impact on the breeding strategy, deployment and testing procedures of *P. patula* in the region.

7.5.2 Quantify potential impact under various scenarios

7.5.2.1 Some predictable GxE have been identified in the previous chapter. Some models have been proposed using, amongst other variables, the median monthly precipitation in October (OCTMEDP) and the Potential evaporation for June (JUNPEV). These include a simple model using one variable with two defined regions and another model with two variables and four defined regions. Both models were able to classify regions such that a difference of around 0.11 between the Type B genetic correlations within the same regions and the Type B genetic

correlations between different regions. Consideration needs to be given to what sort of options are viable using regions defined in such a way and with such relatively modest differences. In other words it is necessary to quantify the sort of gains possible utilizing this sort of information for breeding and deployment.

7.5.2.2 Methodology

The methodology to be utilized is one developed and proposed by (Hodge, 1996). A description of the methodology follows:-

1. We assume we have a regionalisation model with the following parameters:-
Based on OCTMEDP we have 2 equal regions with a Type B genetic correlation of 0.77 within tests in the same region and 0.66 between tests across the 2 defined regions. The average Type B genetic correlation for the entire area was estimated at 0.71.
2. We have half-sib progeny tests as outlined in the previous chapters and wish to predict parental breeding values to establish a new production population. We will assume the variances from one test to another are homogenous. Therefore we can consider $F_{ik} = f_k + fe_{ik}$ where f_k = effect of the k^{th} family which is consistent across environments, and fe_{ik} = interaction effect of the k^{th} family in the i^{th} test.
3. The parameters are derived from within provenance genetic parameter estimates for all the CAMCORE *P. patula* derived from this study as follows:-

$$\begin{aligned} \mu &= 0.034m^3 \\ \text{Var}(F_{ik}) &= \sigma_f^2 = 0.000011 \\ \text{Var}(P_{ijk}) &= \sigma_p^2 = 0.000018 \\ \text{Var}(w_{ijkl}) &= \sigma_w^2 = 0.000175 \end{aligned}$$

This equates to a single site heritability of 0.166.

4. We will assume a breeding population of 500 and will select 20 to be included in a new production population. This will equate to an intensity of selection, symbolized by i , of 2.145.
5. We will need to compare the option of a 'single population' strategy with selections for the entire area to a 'regionalisation' strategy where we have defined two regions – A & B (see 1. Above).
6. Breeding values will be predicted using either single values g_{AB} for the entire region or g_A and g_B for each region separately. If these breeding values for the selections are derived from a selection index, we can calculate percent genetic gain using the following equation (Falconer, 1981):

$$\Delta g = i [\text{Var}(\hat{g})]^{1/2} (0.034)^{-1} 100\%$$

- Where Δg = genetic gain in percent;
 i = standardized selection intensity
 $\text{Var}(\hat{g})$ = variance of predicted breeding values

0.034 = overall mean for volume growth at 5 years

With infinite testing $\text{Var}(\hat{g}) = \text{Var}(g)$ which equates to the total amount of genetic variance available to be utilized.

7.5.2.3 A comparison of theoretical gains for 'single population' versus 'regionalisation'.

A theoretical scenario comparing a 'single population' with a 'regionalisation' approach is as follows:

$\text{Var}(g)$ can be calculated for the first situation assuming 'single population' in one region with an overall Type B genetic correlation of 0.71 as,

$$\text{Var}(g) = 0.71 * (4\sigma_f^2) = 0.0000312,$$

And the overall total theoretical percentage genetic gain possible as,

$$\begin{aligned} \Delta g &= i [\text{Var}(g)]^{1/2} (0.034)^{-1} 100\% \\ &= 2.145 * (0.0000312)^{1/2} * (0.034)^{-1} * 100 \\ &= 35.3\% \end{aligned}$$

whereas for two regions using the 'regionalisation' strategy with Type B genetic correlations of 0.77 between tests in the same region and predicting separate breeding values for each region, the $\text{Var}(g)$ can be calculated as,

$$\text{Var}(g) = 0.77 * (4\sigma_f^2) = 0.0000339,$$

And the gain in each region as,

$$\begin{aligned} \Delta g &= i [\text{Var}(g)]^{1/2} (0.034)^{-1} 100\% \\ &= 2.145 * (0.0000339)^{1/2} * (0.034)^{-1} * 100 \\ &= 36.7\% \end{aligned}$$

This gives a maximum possible additional potential gain with regionalisation of,

$$\text{Gain}_{(\text{regions})} - \text{Gain}_{(\text{single})} = 36.7 - 35.3 = 1.5\%$$

7.5.2.4 There are ways that this upper limit can be increased. These include increasing the population size and then increasing the selection intensity, or improving the predictability of the GxE and in this way define regions more effectively. Both of these are theoretically attainable and indeed the possible gain can be compared when either of these is further manipulated. A scenario where the selection intensity is increased to 20 out of 1000 ($i = 2.421$) and the regions are defined more accurately so that we are able to discriminate between 'same' and 'different' regions with a difference of 0.2 ($r_{\text{Bg same}} = 0.81$) are presented in table 7.5.1.

Table 7.5.1: Theoretical gains possible under infinite testing for scenarios where the selection intensity is increased and the GxE is better defined.

Scenarios	Gain for....		
	Single population	Regionalisation	Percentage increase in gain
$i = 2.145; r_{Bgsame} = 0.77^{**}; r_{Bgdiff} = 0.66$	35.3	36.7	1.5
$i = 2.421; r_{Bgsame} = 0.77; r_{Bgdiff} = 0.66$	39.8	41.4	1.6
$i = 2.145; r_{Bgsame} = 0.81; r_{Bgdiff} = 0.61$	35.3	37.7	2.4
$i = 2.421; r_{Bgsame} = 0.81; r_{Bgdiff} = 0.61$	39.8	42.5	2.7

**Represents the example in the text and what may be currently possible with the knowledge derived from this study.

7.5.2.5 The examples utilized are considered realistic and give a good idea of the sort of maximum gains possible. These may represent reasonable boundaries on what is feasible in a practical breeding programme. These gains are however, theoretical because breeders have cost constraints and are limited to a small number of actual progeny tests and thus cannot achieve this maximum. With the above background in place it is possible to now examine and compare possible gains using a more 'realistic' situation. The 1.7 – 3.0% gain calculated above could thus be considered the upper limit under the scenarios given above.

7.5.2.6 We consider a more realistic scenario given financial constraints on resources. It is assumed that two regions are defined as in 7.5.2.2 above. The overall average Type B genetic correlation is 0.70 and the Type B genetic correlations for tests in the same regions are 0.77 and between regions are 0.66. The \hat{g} is calculated using a selection index and a correlation of g and \hat{g} ($\text{Corr}(g, \hat{g})$) can then be calculated using the genetic parameters that are assumed to be known in the process (White and Hodge, 1989). The gain can then be calculated for each scenario using varying numbers of test sites and comparing to the $\text{Corr}(g, \hat{g})$. A $\text{Corr}(g, \hat{g})$ of around 90% was considered reasonable as the correlation increases slowly with more tests beyond this level (Hodge, 1996). The tests were assumed to be distributed evenly in the two regions and the designs were assumed to be randomized complete block designs with 6 blocks and 5 trees/family / block. The same genetic parameters as described above were assumed for both regions and both regions were assumed to be of equal size and productivity. Varying any of these factors will change the results and this can be done to examine the possibilities but they are unlikely to change the differences in gain substantially. The results for these three scenarios are presented in table 7.5.2.

Table 7.5.2: Numbers of half-sib tests per family and expected gain for three selection scenarios. Gain1 – one region but using information such as the Type B genetic correlation from two regions to calculate an overall gain; Gain2 – two separate regions with separate breeding values calculated for each region.

Tests	Overall*	Region	
	Gain1	Gain2	Gain2 – Gain1
2	26.40	27.13	0.74
4	29.69	30.61	0.91
6**	31.10	32.13	1.03
8	31.88	33.01	1.12
10	32.38	33.58	1.20
12	32.73	33.99	1.26
14	32.98	34.30	1.31
16	33.18	34.54	1.36
18	33.33	34.73	1.40
20	33.46	34.89	1.44

*Overall breeding values but using regional parameters

**Corr(g,ĝ) is around 0.90.

7.5.3 Discussion

7.5.3.1 The theoretical estimations of genetic gain ranging from 1.5 – 2.7% can be considered the upper limits of what may be attainable when considering realistic scenarios. In addition to increasing the selection intensity and defining predictable GxE better, some other factors can also influence these gains. The assumptions used in the above estimates included equal size areas and productivity for each region, as well as limiting the number of defined regions to two. Certainly all of these can be manipulated and will have an effect on the achievable gains but all of them hinge on one key factor – reliably defining predictable GxE. This probably represents the single largest constraint in making more progress with GxE and is the one aspect where this study was only marginally successful. This can be clearly seen by the relatively large increase in gain possible when the differences in the prediction of GxE between regions is increased (Table 7.5.1).

7.5.3.2 The genetic gains estimated when considering the more realistic situation of testing families under a limited number of progeny tests are more modest and even with 20 tests don't exceed 1.5%. Again the scenario utilized looks at possible differences in Type B genetic estimates of 0.11 between 'same' and 'different' regions. This was considered possible with our current understanding of the factors likely to effect the GxE variance. These calculations can thus be considered reasonably realistic to allow planning and assessments of the gains attainable versus the resources spent. In practice, testing individual families in more than 6 progeny tests is likely to be prohibitively expensive and the gains at that level were around 1.0%.

7.5.3.3 The system as developed here allows one to look at different scenarios and make informed decisions on where resources should be spent. Some of the following questions can be posed and answered. Do we split up our breeding and / or deployment populations into different regions and what is the gain achievable for each scenario? How many progeny tests should we plant and in what ratios in each region? If regions are of different sizes and / or represent different site qualities, to what extent should the limited progeny testing resources be spent on the different sites and in what proportions? These questions can be posed and estimates given which will allow realistic planning under the financial constraints which are present in all breeding programs.

7.5.4 Breeding strategy considerations

7.5.4.1 The regionalisation of breeding populations for *P. patula* in Southern Africa on the basis of the GxE identified in this study alone is unlikely to be an attractive option. There are considerable costs associated with having two or more breeding populations and the gains predicted here do not appear to justify this.

7.5.4.2 There may however be many other reasons for establishing separate breeding populations or regions. It may be important to breed for different traits or specifically for separate end products – for example a particular region may be supplying a specific mill. An understanding of the GxE and possible regions proposed here may thus be utilized in addition to other factors in establishing separate regions and breeding populations or in delineating the boundaries of regions.

7.5.4.3 Allied to the above, regionalisation may also yield significantly higher gains when there are specific problems or diseases on particular sites (Carson, 1991). The gains achievable for growth will be considerably reduced if other selection criteria such as disease or pest resistance are included because of problems on certain sites.

7.5.4.4 On the other hand, the evidence presented in this study gives breeders in the region some quantification as to the amount of reactive families are likely to be present. The estimates have varied between 10 and 40%. A figure of 40% appears at first glance to be rather high but many of these are not among the better performers and also include genotypes that did not exhibit rank change. If all these factors are taken into account it may be more attractive to breed for stability and select best overall performers.

7.5.4.5 Finally, GxE can be utilized empirically, without actually having absolute confidence in the environmental boundaries of the regions, by using a multiple population breeding strategy with diversified populations (Barnes, 1995). Populations are constituted to create new differences by using differences in the environment at the population level. This strategy creates diversified populations which can then allow breeders to control and minimize inbreeding at a population level.

7.5.5 Deployment strategy considerations

7.5.5.1 Even if gains are not attractive enough to warrant the establishment of separate breeding programs, breeders may wish to consider utilizing this information in the deployment or production of genotypes or populations (Hodge, 1996). This may be especially true as gains become more attractive with increased selection intensity. The use of commercial full-sib families and even clones for *P. patula* is being actively pursued by several of the larger forestry companies in the region. Realizing even small marginal gains under these circumstances is likely to be worth considering. A gain of 1% on overall productivity will translate into significant benefits.

7.5.5.2 In addition, the information on reactive genotypes and GxE can still be utilized to maximize gain by identifying families that do differentially better on better quality sites. This has been used successfully with *P. taeda* in the USA where it has been demonstrated that certain families are reactive but perform relatively better as resources become less limiting (McKeand et al., 1997), (Duzan and Williams, 1988). Indeed, this has been suggested as a possibility for *P. patula* in the Mpumalanga region of South Africa (Snedden and Verry, 1999). The results of the regression analysis with a range of families analyzed in this study certainly suggest that this strategy can be successfully utilized.

7.5.6 Implications for testing

7.5.6.1 Studies of GxE can give good estimates of the number of tests required to achieve desired gains. Several previous publications have suggested numbers of 3 – 5 tests as a good balance for achieving gain and utilizing resources effectively (Lindgren, 1984), (Carson, 1991) and (Johnson, 1997).

7.5.6.2 Another approach suggested has been to achieve a target level of correlation between predicted breeding values and unobservable true breeding values of 90% for selecting number of

required tests (Hodge, 1996). This is the approach used here and using levels of GxE identified from this study a number of around 6 tests per family is suggested (Table 7.5.2).

7.5.6.3 Furthermore, some studies have attempted to identify criteria that would allow the ‘*a priori*’ selection of good test sites (Carson, 1991). Characteristics of ‘good’ selection sites had rapid growth, high heritability and high phenotypic variance. In hindsight these characteristics would seem logical but in practice, besides the criteria of rapid growth it would probably be difficult to select sites for high heritabilities and large phenotypic variance.

7.5.7 Future considerations

7.5.7.1 At the end of such a study is often instructive to attempt to examine ways to further improve our knowledge of GxE. Indeed, it may be worth posing the question of whether we will ever gain a handle on GxE at the intraspecific level. Several authors suggest that we will not (Barnes et al., 1984), (Matheson and Cotterill, 1990). They contend that there are so many variables of importance especially for characteristics like growth that are under multigenic control, that it would require a vast number of tests. As stated by (Barnes et al., 1984); ‘It is probably only realistic to expect to detect, explain and use GxE when a single factor in the environment affects an economically important trait in a predictable manner’.

7.5.7.2 In addition, any further work on this issue is likely to consume resources which, when looking at potential gain may be best invested elsewhere. Perhaps the issue might become easier to study at the clonal level when the genotype itself is constant and the breeder has developed a small number of potentially valuable clones for commercial use.

7.5.7.3 One issue that is apparent from this study is the constant need for more sampling of the environment. However, establishing expensive replicated progeny tests just does not appear to be a realistic path for moving forward on this issue. An interesting idea raised by (Wright, 1973), and apparently discussed by him with scientists such as R. A. Fisher and Gene Namkoong was to design a trial with several ‘key’ genotypes, probably clones or at least full-sib families, over a large number of sites as single plots. He suggested that such an experiment could yield strong data on performance of genotypes over a large range of sites. One would lose the opportunity to measure the interaction between two sites in such a design but it appears from the countless studies of GxE that these interactions may defy realistic interpretation anyway. In addition, such an experiment could be assembled over a number of years as breeders establish annual tests for other purposes. This would make them relatively inexpensive to establish and maintain because no new sites would need to be found and managed separately. Analysis of such data would be

empirical, much like a site factor study but with far greater control of both genetics and manageable factors in the environment. This may be something worth exploring?!

CHAPTER 8 – LITERATURE CITED

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Appendix 1: Summary information for CAMCORE *P. patula* tests in South Africa, included in Analyses

Test code	Region	Location	Lat.	Long.	Alt. (m)	MAP (mm)	MAT (°C)	Age (yrs)	Provenances represented – prov. codes in appendix 2
20-18-01J	N.E.Cape	Commonage	31°02'S	28°19'E	1480	757	14.7	8	1, 2, 3, CON
20-18-02E		Commonage	31°02'S	28°19'E	1480	757	14.7	8	1, 4, 5, 6, 7, CON
20-18-05K		Commonage	31°02'S	28°19'E	1480	757	14.7	8	1, 8, 10, 11, 12, 13, CON
20-18-06D		Commonage	31°02'S	28°19'E	1480	757	14.7	8	1, 8, 10, 11, 12, 13, CON
20-18-07A		Commonage	31°02'S	28°19'E	1480	757	14.7	8	1, 8, 9, 10, 11, 12, 13, CON
20-07-01L	Kwa-ZuluNtl	Maxwell	30°02'S	29°56'E	1350	817	16	8	1, 2, 3, CON
20-07-02D		Maxwell	30°02'S	29°56'E	1350	817	16	8	1, 4, 5, 6, 7, CON
20-07-05L		Maxwell	30°02'S	29°56'E	1350	817	16	8	1, 8, 10, 11, 12, 13, CON
20-07-06E		Maxwell	30°02'S	29°56'E	1350	817	16	8	1, 8, 10, 11, 12, 13, CON
20-07-07D		Maxwell	30°02'S	29°56'E	1350	817	16	8	1, 8, 9, 10, 11, 12, 13, CON
PV34C1		Goodhope	29°55'S	29°42'E				8	1, 2, 3, CON
PV34C2		Goodhope	29°55'S	29°42'E				8	8, 10, 11, 12, 13, CON
20-07-04C	Mpumalanga	Helvetia E7	25°32'S	30°22'E	1700	770	14.7	3	1, 2, 3, CON
20-07-09B		Helvetia E7	25°32'S	30°22'E	1700	770	14.7	3	15, 16, 17, 18, CON
20-07-10B		Helvetia E7	25°32'S	30°22'E	1700	770	14.7	3	1, 19, 20, CON
20-07-08C		Helvetia A39	25°34'S	30°22'E				7	1, 15, 16, 17, 18, 19, CON
20-07-15E		Hlelo	26°57'S	30°41'E				3	22, 23, CON
20-10-01A		Tweefontein	25°03'S	30°46'E	1150	1274		8	1, 2, 3, CON
20-10-02A		Tweefontein	25°03'S	30°46'E	1150	1274		8	1, 4, 5, 6, 7, CON
20-10-03A1		Tweefontein	25°03'S	30°46'E	1150	1274		8	1, 4, 5, 6, 7, CON
20-10-04A1		Tweefontein	25°03'S	30°46'E	1150	1274		8	1, 2, 3, CON
20-10-05E1		Tweefontein	25°03'S	30°46'E	1150	1274		8	1, 8, 10, 11, 12, 13, CON
20-10-06B1		Tweefontein	25°03'S	30°46'E	1150	1274		8	1, 8, 10, 11, 12, 13, CON
20-10-07B1		Tweefontein	25°03'S	30°46'E	1150	1274		8	1, 8, 9, 10, 11, 12, 13, 14, CON
20-10-08A		Tweefontein	25°03'S	30°46'E	1150	1274		5	1, 15, 16, 17, 18, 19, CON
20-10-10C		Tweefontein	25°03'S	30°46'E	1150	1274		8	1, 19, 20, CON
20-10-15I		Tweefontein	25°03'S	30°45'E				3	22, 23, CON
PV34B1		Magsleigh	25°12'S	30°46'E				8	1, 2, 3, 4, 5, 6, CON
PV34B2		Magsleigh	25°12'S	30°46'E				8	8, 11, 12, 13, CON
20-10-01B		Jessievale	26°14'S	30°31'E	1730	921	14	8	1, 2, 3, CON
20-10-02B		Jessievale	26°14'S	30°31'E	1730	921	14	8	1, 4, 5, 6, 7, CON
20-10-03A2		Jessievale	26°14'S	30°31'E	1730	921	14	8	1, 4, 5, 6, 7, CON
20-10-04A2		Jessievale	26°14'S	30°31'E	1730	921	14	8	1, 2, 3, CON
20-10-05E2		Jessievale	26°14'S	30°31'E	1730	921	14	8	1, 8, 10, 11, 12, 13, CON
20-10-06B2		Jessievale	26°14'S	30°31'E	1730	921	14	8	1, 8, 10, 11, 12, 13, CON
20-10-07B2		Jessievale	26°14'S	30°31'E	1730	921	14	8	8, 9, 10, 11, 12, 13, 14, CON
20-10-05F		Mariti	24°55'S	30°57'E	980	1316		5	1, 8, 10, 11, 12, 13, CON
20-18-01H		Jessievale	26°12'S	30°29'E	1691	931	14	5	1, 2, 3, CON
20-18-08B		Jessievale	26°12'S	30°29'E	1691	931	14	5	1, 15, 16, 17, 18, 19, CON
20-18-09A		Jessievale	26°12'S	30°29'E	1691	931	14	5	15, 16, 17, 18, CON
R203	Swaziland	Usutu S1	26°22'S	30°55'E				3	22, CON

*CON represents other controls.

Appendix 2: Details of provenances collected by CAMCORE represented with associated provenance codes.

Provenance	Prov Code	State	Lat	Long	Alt. (m)	MAP (mm)	Test representation
Carrizal de Bravo	14	Guerrero	17°35'N	99°51'W	1980-2440	1209	20-10-07B1, 20-10-07B2
Cumbre Muridores	18	Higdalgo	20°19'N	98°21'W	2380-2480	1860	20-10-08A, 20-10-08B, 20-07-09B, 20-18-09A
La Cruz	17	Higdalgo	20°17'N	98°18'W	2300-2450	1869	20-10-08A, 20-10-08B, 20-07-09B, 20-18-09A
La Encarnación	16	Higdalgo	20°45'N	99°13'W	2400-2650	1200	20-10-08A, 20-10-08B, 20-07-09B, 20-18-09A
Zacualtipán	12	Higdalgo	20°39'N	98°40'W	1980-2200	2047	20-07-05L, 20-10-05E1, 20-10-05E2, 20-10-05F, 20-18-05K, 20-07-06E, 20-10-06B1, 20-10-06B2, 20-18-06D, 20-07-07D, 20-10-07B1, 20-10-07B2, 20-18-07A
Cuajimoloyas	9	Oaxaca	17°11'N	96°26'W	2450-2770	1135	20-07-07D, 20-10-07B1, 20-10-07B2, 20-18-07A
El Manzanal	4	Oaxaca	16°06'N	96°33'W	2350-2660	1348	20-07-02D, 20-10-02A, 20-10-02B, 20-18-02E, 20-10-03A1, 20-10-03A2
El Tlacuache	5	Oaxaca	16°44'N	97°09'W	2300-2620	2000	20-07-02D, 20-10-02A, 20-10-02B, 20-18-02E, 20-10-03A1, 20-10-03A2
Ixtlán	6	Oaxaca	17°24'N	96°27'W	2600-2870	1750	20-07-02D, 20-10-02A, 20-10-02B, 20-18-02E, 20-10-03A1, 20-10-03A2
Santa Maria Papalo	7	Oaxaca	17°49'N	96°48'W	2270-2720	1100	20-07-02D, 20-10-02A, 20-10-02B, 20-18-02E, 20-10-03A1, 20-10-03A2
Pinal de Amoles	11	Queretaro	21°07'N	99°41'W	2380-2550	1350	20-07-05L, 20-10-05E1, 20-10-05E2, 20-10-05F, 20-18-05K, 20-07-06E, 20-10-06B1, 20-10-06B2, 20-18-06D, 20-07-07D, 20-10-07B1, 20-10-07B2, 20-18-07A
Llano Las Carmonas	13	Puebla	19°48'N	97°54'W	2530-2880	1097	20-07-05L, 20-10-05E1, 20-10-05E2, 20-10-05F, 20-18-05K, 20-07-06E, 20-10-06B1, 20-10-06B2, 20-18-06D, 20-07-07D, 20-10-07B1, 20-10-07B2, 20-18-07A
Conrado Castillo	8	Tamaulipas	23°56'N	99°28'W	1500-2060	1012	20-07-05L, 20-10-05E1, 20-10-05E2, 20-10-05F, 20-18-05K, 20-07-06E, 20-10-06B1, 20-10-06B2, 20-18-06D, 20-07-07D, 20-10-07B1, 20-10-07B2, 20-18-07A
El Cielo	15	Tamaulipas	23°04'N	99°14'W	1600-1730	1200	20-10-08A, 20-10-08B, 20-07-09B, 20-18-09A
Tlacotla	10	Tlaxcala	19°40'N	98°05'W	2750-2915	1097	20-07-05L, 20-10-05E1, 20-10-05E2, 20-10-05F, 20-18-05K, 20-07-06E, 20-10-06B1, 20-10-06B2, 20-18-06D, 20-07-07D, 20-10-07B1, 20-10-07B2, 20-18-07A
Corralitla	3	Veracruz	18°38'N	97°06'W	2000-2230	1500	20-07-01L, 20-10-01A, 20-10-01B, 20-18-01H, 20-18-01J, 20-10-03A1, 20-10-03A2, 20-07-04C, 20-10-04A1, 20-10-04A2
Cruz Blanca	19	Veracruz	19°39'N	97°09'W	2500	1347	20-10-08A, 20-10-08B
Ingenio del Rosario	2	Veracruz	19°31'N	97°06'W	2770-2870	1346	20-07-01L, 20-10-01A, 20-10-01B, 20-18-01H, 20-18-01J, 20-07-04C, 20-10-04A1, 20-10-04A2
Potrero de Monroy	1	Veracruz	20°24'N	98°25'W	2320-2480	1350	Included in most – see appendix 1
Sierra Huayococotla	22	Veracruz	20°29'N	98°28'W	1840-2860	1405	20-07-15E, 20-10-15L, R203
Acaxochitlan	23						20-07-15E, 20-10-15L
Calcahualco	20	Veracruz	19°07'N	97°06'W	2350-2400	2020	20-0710B, 20-10-10C

*Details from [Dvorak, 2000 #593]

Appendix 3: Details of treatments entered in all 10 tests of the CAMCORE 01 & 04 series – (1) = Potrero de Monroy, (2) = Ingenio del Rosario, (3) = Corralitla and (SA) = South African genetic checks or controls.

Prov	Fam	Test										Nr. of Trials
		20-10-01A	34B1	20-10-01B	20-18-01H	34C1	20-07-01L	20-18-01J	20-10-04A1	20-07-04C	20-10-04A2	
1	1		1						1	1	1	4
1	2	1	1	1	1		1	1				6
1	3		1						1	1	1	4
1	4								1	1	1	3
1	5	1		1	1		1	1	1	1	1	8
1	6	1	1	1	1	1	1	1				7
1	7	1	1	1	1	1	1	1				7
1	8	1		1	1		1	1				5
1	9	1	1	1	1	1	1	1				7
1	10	1		1	1		1	1	1	1	1	8
1	11	1		1	1		1	1	1	1	1	8
1	12	1	1	1	1	1	1	1				7
1	13	1			1		1					3
1	14	1	1	1	1		1	1				6
1	15									1		1
1	16	1	1	1	1		1	1				6
1	17	1			1							2
1	18		1						1	1	1	4
1	19								1	1	1	3
1	20				1							1
1	21	1	1	1	1	1	1	1				7
1	22	1		1	1		1	1				5
1	23		1						1	1	1	4
1	24								1	1	1	3
1	25	1	1	1	1	1	1	1				7
1	26	1	1	1	1		1	1				6
1	27	1	1	1	1	1	1	1				7
1	28				1					1		2
1	29		1			1			1	1	1	5
1	30		1						1	1	1	4
1	31		1						1	1	1	4
2	32	1			1			1				3
2	33	1			1		1					3
2	34		1						1	1	1	4
2	35	1	1	1	1		1	1				6
2	36	1		1	1		1	1				5
2	37	1		1	1			1				4
2	38	1	1	1	1	1	1	1				7
2	39								1	1	1	3
2	40								1	1	1	3
2	41	1		1	1		1	1	1	1		7
2	42		1						1	1	1	4
2	43		1						1	1	1	4
2	44	1		1	1		1	1	1	1	1	8

2	45	1		1	1		1	1				5
2	46	1		1	1		1	1	1	1	1	8
2	47		1						1	1	1	4
2	48	1	1	1	1	1	1	1				7
2	49	1	1	1	1		1		1	1		7
2	50	1	1	1	1	1	1	1				7
2	51	1	1	1	1	1	1	1				7
2	52	1	1	1	1	1	1	1				7
2	53	1		1	1		1	1				5
3	54	1	1	1	1	1	1	1				7
3	55	1	1	1	1	1	1	1				7
3	56	1	1	1	1	1	1	1				7
3	57	1	1	1	1	1	1	1				7
3	58	1	1	1	1	1	1	1				7
3	59	1	1	1	1	1	1	1	1	1	1	10
3	60		1						1	1	1	4
3	61	1	1	1	1	1	1	1				7
3	62	1	1	1	1	1	1	1	1	1	1	10
3	63	1	1	1		1	1	1				6
3	64	1	1	1	1	1	1	1				7
3	65		1						1	1	1	4
3	66	1	1	1	1	1	1	1	1	1	1	10
3	67	1	1	1	1	1	1	1				7
3	68									1		1
3	69	1		1	1		1	1	1	1	1	8
3	70								1	1	1	3
3	71	1	1	1	1		1	1				6
3	72		1						1	1	1	4
3	73	1	1	1	1	1	1	1				7
3	74	1	1	1	1		1	1				6
3	75		1						1	1	1	4
SA	996	1	1	1	1	1	1	1	1	1	1	10
SA	997	1	1	1	1	1	1	1	1	1	1	10
SA	998	1		1		1	1	1	1		1	7
SA	999	1	1	1	1	1	1	1	1	1	1	10

*996 = unimproved SA landrace; 997 = 1st gen. Clonal Seed Orchard mix; 998 = 1st gen. Seedling Seed Orchard mix; 999 = 2nd gen. Clonal Seed Orchard mix.

Appendix 4: Details of treatments entered in all 7 tests of the CAMCORE 02 & 03 series – (1) = Potrero de Monroy, (4) = El Manzanal, (5) = El Tlacuache, (6) = Ixtlan, (7) = Santa Maria Papalo and (SA) = South African genetic checks or controls.

Prov	Fam	Test						PV34B1	Nr. of Trials
		20-10-02A	20-10-02B	20-07-02D	20-18-02E	20-10-03A1	20-10-03A2		
1	1							1	1
1	2							1	1
1	3							1	1
1	5	1	1	1	1	1	1		6
1	6							1	1
1	7							1	1
1	9							1	1
1	10	1	1	1	1	1	1		6
1	11	1	1	1	1	1	1		6
1	12							1	1
1	14							1	1
1	16							1	1
1	18							1	1
1	21							1	1
1	23							1	1
1	25							1	1
1	26							1	1
1	27							1	1
1	29							1	1
1	30							1	1
1	31							1	1
4	77					1	1	1	3
4	78	1	1	1	1			1	5
4	79					1	1	1	3
4	80	1	1	1	1				4
4	81					1	1		2
4	83	1	1	1	1			1	5
4	84					1	1	1	3
4	85	1	1	1	1			1	5
4	86	1	1	1	1				4
4	87	1	1	1	1			1	5
4	88	1	1	1	1			1	5
4	89					1	1		2
4	90	1	1	1	1				4
4	91					1	1	1	3
4	93					1	1	1	3
4	94					1			1
4	95	1	1	1	1			1	5
4	96					1	1		2
4	97					1			1
4	98	1	1	1	1			1	5
4	99		1		1				2
4	100	1	1	1	1			1	5
4	102	1	1	1	1			1	5

4	103					1	1	1	3
5	107	1	1	1	1	1	1		6
5	112					1		1	2
5	114					1	1		2
5	115					1	1		2
5	118	1	1	1	1			1	5
5	119	1	1	1	1	1	1	1	7
5	120					1	1		2
5	121	1	1	1	1	1	1	1	7
5	123	1	1	1	1	1	1	1	7
5	124	1	1	1	1	1	1	1	7
5	125	1	1	1	1				4
5	126	1	1	1	1	1	1	1	7
5	128	1	1	1	1				4
5	130	1	1	1	1	1	1		6
5	131	1	1	1	1			1	5
6	132					1	1		2
6	133					1	1		2
6	134	1	1	1	1			1	5
6	135	1	1	1	1			1	5
6	136					1			1
6	138	1	1	1	1			1	5
6	141	1	1	1	1				4
6	143					1			1
6	144	1	1	1	1				4
6	145	1	1	1	1				4
6	146					1	1		2
6	147	1	1	1	1			1	5
6	148	1	1	1	1	1	1	1	7
6	149	1	1	1	1			1	5
6	150	1	1	1	1	1	1		6
6	151	1	1	1	1			1	5
6	152	1	1	1	1	1	1	1	7
6	153	1	1	1	1			1	5
6	154	1	1	1	1				4
6	155					1	1		2
6	156	1	1	1	1			1	5
6	157	1		1					2
6	158					1			1
7	159	1	1	1	1				4
7	160	1	1	1	1	1	1		6
7	161	1	1	1	1				4
7	162					1			1
7	163	1	1	1	1	1	1		6
7	164	1	1	1	1				4
7	165	1	1		1				3
7	166	1	1	1	1				4
7	167	1	1	1	1	1	1		6
7	168	1	1	1	1				4
7	169	1	1	1					3

7	170	1	1	1	1				4
7	171	1	1	1	1	1	1		6
7	172	1	1	1	1				4
7	173					1	1		2
7	174	1	1	1	1				4
7	175					1	1		2
7	176					1	1		2
7	177	1	1	1	1				4
7	178					1	1		2
7	179					1	1		2
7	180					1			1
7	181					1			1
7	182					1			1
<hr/>									
SA	996	1	1	1	1	1	1	1	7
SA	997	1	1	1	1	1	1	1	7
SA	998	1	1	1	1	1	1		6
SA	999	1	1	1	1	1	1	1	7

*996 = unimproved SA landrace; 997 = 1st gen. Clonal Seed Orchard mix; 998 = 1st gen. Seedling Seed Orchard mix; 999 = 2nd gen. Clonal Seed Orchard mix.

Appendix 5: Details of treatments entered in all 15 tests of the CAMCORE 05, 06 & 07 series – (1) = Potrero de Monroy, (8) = Conrado Castillo, (9) = Cuajimoloyas, (10) = Tlacotla, (11) = Pinal de Amoles, (12) = Zacualtipan, (13) = Llano de las Carmonas and (14) = Carrizal de Bravo.

Prov	Fam	Test												PV 34B2	PV 34C2	Nr. of Trials
		20- 10- 05F	20- 10- 05E1	20- 10- 05E2	20- 07- 05L	20- 18- 05K	20- 10- 06B1	20- 10- 06B2	20- 07- 06E	20- 18- 06D	20- 10- 07B1	20- 10- 07B2	20- 07- 07D			
1	5	1	1	1	1	1	1	1	1	1	1	1	1			12
1	8	1														1
1	10	1	1		1	1	1		1	1	1		1	1		10
1	11	1	1	1	1	1	1	1	1	1	1		1	1		12
1	28	1														1
8	223	1	1	1			1		1		1		1	1		8
8	224						1	1	1	1	1	1	1	1	1	10
8	225	1	1	1	1	1									1	7
8	226						1	1	1	1	1	1	1	1	1	10
8	227	1	1	1	1	1									1	7
8	228	1	1	1	1	1									1	7
8	229						1	1	1	1	1	1	1	1	1	10
8	230	1	1	1	1	1									1	6
8	231	1	1	1	1	1									1	6
8	232	1	1	1	1	1									1	7
8	233	1	1	1	1	1									1	7
8	234	1	1	1	1	1									1	7
8	235						1	1		1						3
8	236						1	1	1							3
8	237	1	1	1	1	1									1	7
8	238	1	1	1	1	1									1	7
8	239	1	1	1	1	1									1	7
8	240	1	1	1	1	1									1	7
8	241	1	1	1	1	1									1	7
8	242	1	1	1	1	1									1	7
8	243	1	1	1	1	1									1	7
8	244						1	1	1	1					1	6
8	245	1	1	1	1	1									1	6
8	246						1	1	1	1	1	1	1	1	1	10
8	247						1	1	1	1					1	6
9	183										1					1
9	190										1					1
9	191										1	1	1	1		4
9	192										1			1		2
9	193										1					1
9	194										1	1	1	1		4
9	195										1		1			2
9	196										1					1
9	198										1					1
10	289	1	1	1	1	1										5
10	290	1	1	1	1	1										5
10	291						1				1					2

12	260	1															1
12	261	1	1	1	1	1											5
12	262	1	1	1	1	1										1	6
13	263						1	1	1	1	1	1	1	1	1		9
13	264	1	1	1	1	1									1	1	7
13	265	1	1	1	1												4
13	266	1	1													1	3
13	267	1	1														2
13	268						1	1	1	1					1	1	6
13	269										1	1	1	1	1	1	6
13	270	1	1	1	1	1									1		6
13	271						1	1	1	1	1		1	1			7
13	272	1	1	1	1	1									1	1	7
13	273										1	1	1				3
13	275										1	1	1	1			4
13	276						1	1	1	1	1	1	1	1			8
13	277						1	1	1	1					1		5
13	278						1	1	1	1					1	1	6
13	279						1				1						2
13	280	1	1	1	1	1											5
13	281						1	1			1		1	1			5
13	282						1										1
13	283						1	1		1							3
13	284	1	1	1	1	1									1	1	7
13	285	1	1	1	1	1									1	1	7
13	286	1	1	1	1	1									1	1	7
13	287						1	1	1	1	1	1	1	1	1	1	10
13	288						1	1	1	1					1		5
14	310										1	1					2
14	313										1						1
SA	996		1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
SA	997		1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
SA	998	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	15
SA	999	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	15

*996 = unimproved SA landrace; 997 = 1st gen. Clonal Seed Orchard mix; 998 = 1st gen. Seedling Seed Orchard mix; 999 = 2nd gen. Clonal Seed Orchard mix.

**Appendix 6: Details of treatments entered in all 5 tests of the CAMCORE 08 & 09 series –
 (1) = Potrero de Monroy, (15) = El Cielo, (16) = La Encarnacion, (17) = La Cruz, (18) =
 Cumbre de Muridores, (19) = Cruz Blanca.**

Prov	Fam	Tests					Nr. of Trials
		20-10-08A	20-07-08C	20-18-08B	20-07-09B	20-18-09A	
1	5	1	1	1			3
1	7	1	1	1			3
1	8	1	1	1			3
1	12	1	1	1			3
1	13	1	1	1			3
1	23	1	1	1			3
1	29	1	1	1			3
15	1287					1	1
15	1288				1		1
15	1289	1	1	1			3
15	1290				1	1	2
15	1291	1	1	1			3
15	1292	1	1	1			3
15	1293					1	1
15	1294				1		1
15	1295	1	1	1			3
15	1296	1	1	1	1	1	5
15	1297	1	1	1	1	1	5
15	1298	1	1	1	1	1	5
15	1299				1	1	2
15	1300	1	1	1	1	1	5
15	1301	1	1	1	1	1	5
15	1302	1	1	1	1	1	5
15	1303				1	1	2
15	1304				1	1	2
15	1305				1	1	2
15	1306				1	1	2
15	1307				1	1	2
15	1308				1	1	2
15	1309				1	1	2
16	1310	1	1	1			3
16	1311	1	1	1			3
16	1312	1	1	1			3
16	1313	1	1	1			3
16	1314	1	1	1			3
16	1315					1	1
16	1316				1		1
16	1317					1	1
16	1318	1	1	1			3
16	1319				1	1	2
16	1320					1	1
16	1321				1		1
16	1322	1	1	1			3
16	1323				1		1

16	1324	1	1	1			3
16	1325	1	1	1			3
16	1326				1	1	2
17	328	1	1	1			3
17	329	1	1	1			3
17	330	1	1	1			3
17	331	1	1	1			3
17	332	1	1	1			3
17	333	1	1	1			3
17	334	1	1	1			3
17	335	1	1	1			3
17	336	1	1	1			3
17	337	1	1	1			3
17	338				1	1	2
17	339				1	1	2
17	340				1	1	2
17	342				1	1	2
17	344				1	1	2
17	345				1	1	2
17	346				1	1	2
17	347				1	1	2
17	348				1	1	2
17	349				1	1	2
17	350				1	1	2
17	351				1	1	2
18	352				1	1	2
18	353				1	1	2
18	354	1	1	1			3
18	355	1	1	1			3
18	356					1	1
18	357	1	1	1			3
18	358				1	1	2
18	359	1	1	1			3
18	360				1	1	2
18	361				1		1
18	362				1	1	2
18	363				1	1	2
18	365	1	1	1			3
18	366				1	1	2
18	367				1	1	2
18	368	1	1	1			3
18	369				1	1	2
18	370	1	1	1			3
18	371	1	1	1			3
18	372	1	1	1			3
18	373	1	1	1			3
18	374				1	1	2
18	375				1	1	2
18	376				1	1	2
18	377				1	1	2

18	378				1	1	2
18	379				1	1	2
18	381					1	1
<hr/>							
19	382	1	1	1			3
19	383	1	1	1			3
19	384	1	1	1			3
19	385	1	1	1			3
19	386	1	1	1			3
19	387	1	1	1			3
19	388	1	1	1			3
19	389	1	1	1			3
<hr/>							
SA	996			1			1
SA	997	1	1	1	1	1	5
SA	998		1		1	1	3
SA	999	1	1		1	1	4

*996 = unimproved SA landrace; 997 = unimproved SA landrace; 998 = 1st gen. Clonal Seed Orchard mix; 999 = 2nd gen. Clonal Seed Orchard mix.

Appendix 7: Details of treatments entered in all 3 tests of the CAMCORE 10 series – (1) = Potrero de Monroy, (19) = Cruz Blanca, (20) = Calchualco.

Prov	Fam	20-10-10C	20-07-10B	20-18-10E	Nr. of Trials
1	5	1	1	1	3
1	8	1	1	1	3
1	23	1	1	1	3
1	28	1	1	1	3
1	29	1	1	1	3
19	390		1	1	2
19	393			1	1
19	394	1	1	1	3
19	396	1			1
19	397		1	1	2
19	401		1	1	2
19	403		1		1
19	405	1			1
19	407	1			1
19	408		1	1	2
19	412		1	1	2
19	413	1	1	1	3
19	415	1	1	1	3
19	416	1	1	1	3
19	417	1	1	1	3
19	418	1	1	1	3
19	419	1	1	1	3
20	420	1	1	1	3
20	423	1	1	1	3
20	427	1	1	1	3
20	429	1	1	1	3
20	432	1	1	1	3
20	434	1	1	1	3
20	438	1	1	1	3
20	441	1	1	1	3
20	443	1	1	1	3
20	444	1	1	1	3
20	445	1	1	1	3
20	447	1	1	1	3
20	449	1	1	1	3
SA	995	1	1		2
SA	998	1			1
SA	999	1	1		2

*999 = unimproved SA landrace; 995 = 1st gen. Clonal Seed Orchard mix; 998 = 2nd gen. Clonal Seed Orchard mix.

Appendix 8: Details of treatments entered in all 3 tests of the CAMCORE 15 series – (1) = Potrero de Monroy, (22) = Sierra Huayococotla, (23) = Acaxochitlan.

Prov	Fam	Tests			Nr. of trials
		20-10-15L	20-07-15E	R 203	
1	12			1	1
1	22			1	1
22	480	1	1	1	3
22	481	1	1	1	3
22	482	1	1	1	3
22	483	1	1		2
22	484	1	1		2
22	485	1	1	1	3
22	486	1	1		2
22	487		1		1
22	488		1	1	2
22	489		1		1
22	490		1	1	2
22	491		1	1	2
22	492	1	1		2
22	493	1	1	1	3
22	494	1	1	1	3
22	495		1	1	2
22	496		1	1	2
22	497		1		1
22	498		1		1
22	499		1		1
22	500		1	1	2
22	501	1			1
22	502	1	1	1	3
22	503	1	1	1	3
22	504	1	1	1	3
22	505	1	1		2
22	506	1	1	1	3
22	507	1	1	1	3
22	508	1			1
22	509	1	1	1	3
22	510	1	1		2
22	511	1	1	1	3
22	512	1	1		2
22	513		1	1	2
22	514		1	1	2
22	515		1		1
22	516		1		1
22	517		1	1	2
22	520	1	1	1	3
22	523	1			1
22	524	1			1
22	525	1			1
22	526	1			1

22	527	1			1
22	533	1			1
22	534	1			1
22	537	1			1
22	538	1			1
22	540	1			1
22	541	1			1
22	544	1			1
22	546	1			1
22	547	1			1
22	548	1			1
22	549	1			1
<hr/>					
23	550	1	1		2
23	551		1		1
23	552		1		1
23	553	1	1		2
23	554		1		1
23	555	1	1		2
23	556	1	1		2
23	557	1	1		2
23	558	1	1		2
23	559	1	1		2
<hr/>					
SA	28			1	1
SA	560	1	1	1	3
SA	561	1	1	1	3
SA	562	1	1	1	3
SA	563	1	1	1	3
SA	993	1	1	1	3
SA	994	1	1		2
SA	995	1	1	1	3
SA	996	1	1		2
SA	997	1	1	1	3
SA	998	1	1		2
SA	999	1	1		2
SA	1074			1	1
SA	9512			1	1
<hr/>					

Appendix 9: A summary of site (Location & climate) details for the Mondi and CSIR trials utilized for the establishment of the GxE models.

Test	Region	Location	Long.	Lat.	Alt.(m)	MAP.(mm)	MAT.(°C)
1/83A	Mpumalanga	Magsleigh	30.79	25.26	1305	1142	17.1
1/83B	Mpumalanga	Driekop	30.81	24.90	1460	1396	15.8
1/83C	Mpumalanga	New Scotland	30.64	26.35	1633	877	14.5
1/83D	KZN	Garfield	31.30	28.53	1086	972	17.0
1/83E	KZN	Excelsior	29.37	29.92	1795	884	13.7
1/83F	KZN	Mahehle	29.90	30.13	1181	957	16.7
1/83H	Eastern Cape	Craigmore	28.17	31.12	1341	751	15.1
PF4005	Mpumalanga	Mac Mac	30.80	24.82	1390	976	16.5
PF4005	Mpumalanga	Wilgeboom	30.95	24.93	980	1134	18.4
PF4006	Mpumalanga	Mac Mac	30.80	24.82	1390	976	16.5
PF4006	Mpumalanga	Jessievale	30.52	26.27	1706	891	14.1
PF4008/9	Mpumalanga	Mac Mac	30.80	24.82	1390	976	16.5
PF4008/9	Mpumalanga	Jessievale	30.52	26.23	1722	933	16.5
PF4012	Mpumalanga	Tweefontein	30.78	25.05	1150	1189	17.6
PF4012	Mpumalanga	Jessievale	30.51	26.32	1722	933	16.5
PF4012	KZN	Weza	29.72	30.60	1023	966	16.4

Appendix 10: A summary of test details for the Mondi and CSIR trials utilized for the establishment of the GxE models.

Test	Organization	Region	Planted	Age	Nr. of Common families*	Design
1/83A	Mondi	Mpumalanga	1983	5	around 200	6 tests/site in a RCB with 5 replications and 6 tree line plots
1/83B	Mondi	Mpumalanga	1983	5	around 200	7 tests/site in a RCB with 5 replications and 6 tree line plots
1/83C	Mondi	Mpumalanga	1983	5	around 200	7 tests/site in a RCB with 5 replications and 6 tree line plots
1/83D	Mondi	KZN	1983	5	around 200	6 tests/site in a RCB with 4 replications and 6 tree line plots
1/83E	Mondi	KZN	1983	5	around 200	6 tests/site in a RCB with 5 replications and 6 tree line plots
1/83F	Mondi	KZN	1983	5	around 200	7 tests/site in a RCB with 5 replications and 6 tree line plots
1/83H	Mondi	Eastern Cape	1983	5	around 200	6 tests/site in a RCB with 5 replications and 6 tree line plots
PF4005	CSIR	Mpumalanga	Feb, 1975	8	47	7x7 lattice with 4replications and 10 tree line pots
PF4005	CSIR	Mpumalanga	Feb, 1975	8	47	7x7 lattice with 4replications and 10 tree line pots
PF4006	CSIR	Mpumalanga	March, 1976	8	38	6x7 lattice with 3 relications and 10 tree line plots
PF4006	CSIR	Mpumalanga	March, 1976	8	38	6x7 lattice with 3 relications and 10 tree line plots
PF4008/9	CSIR	Mpumalanga	March, 1983	8	around 170	6 sets/site in a 7x7 lattice with 8 replications and 6 tree line plots
PF4008/9	CSIR	Mpumalanga	March, 1983	8	around 170	6 sets/site in a 7x7 lattice with 8 replications and 6 tree line plots
PF4012	CSIR	Mpumalanga	Dec.,1990	7	around 100	RCB with 20 replications in single tree plots
PF4012	CSIR	Mpumalanga	Dec.,1990	7	around 100	RCB with 20 replications in single tree plots
PF4012	CSIR	KZN	Jan.,1991	7	around 100	RCB with 20 replications in single tree plots

*All families were open-pollinated with Mondi being from 2nd gen. Parents and the CSIR from 1st gen. parents

Appendix 11: Single-site Heritability estimates (diagonal) and Type B genetic correlations (off diagonal) for volume per tree at 5 years for 7 sites from the Mondi trial series.

Sites	1/83A	1/83B	1/83C	1/83D	1/83E	1/83F	1/83H
1/83A	0.20						
1/83B	1.00	0.20					
1/83C	0.39	0.35	0.17				
1/83D	0.92	0.76	0.70	0.35			
1/83E	0.33	0.55	1.00	0.42	0.12		
1/83F	0.65	1.00	1.00	1.00	1.00	0.14	
1/83H	0.78	0.59	0.53	0.54	0.38	1.00	0.23
Mean r_{Bg}	0.68	0.71	0.66	0.72	0.61	0.94	0.64

Appendix 12: Single-site Heritability estimates (diagonal) and Type B genetic correlations (off diagonal) for volume per tree at 7 / 8 years for 5 sites from the CSIR trial series.

Series	Site	Mac Mac	Wilgeboom	Tweefontein	Jessievale*	Weza
PF4005	Mac Mac	0.83	-	-	-	-
	Wilgeboom	0.70	0.30	-	-	-
PF4006	Mac Mac	0.30	-	-	-	-
	Jessievale*	0.33	-	-	0.26	-
PF4008/9	Mac Mac	0.13	-	-	-	-
	Jessievale*	0.71	-	-	0.17	-
PF4012	Tweefontein	-	-	0.23	-	-
	Jessievale*	-	-	0.89	0.37	-
	Weza	-	-	1.00	0.94	0.18