Remediation of instability in Best Linear Unbiased Prediction (BLUP) in tree breeding populations

by

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DECLARATION

I, the undersigned, hereby declare that this thesis which I hereby submit for the degree Philosophiae Doctor at the University of Pretoria is my own original work and has not previously, in its entirety or in part, been submitted to any other university.

Signature:  . . . . . Date: 9 December 2013 . . . .

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SUMMARY

In most breeding programmes breeders use phenotypic data obtained in breeding trials to rank the performance of the parents or progeny on pre-selected performance criteria. Through this ranking the best candidates are identified and selected for breeding or production purposes. Best Linear Unbiased Prediction (BLUP), is an efficient selection method to use, combining information into a single index. Unbalanced or messy data is frequently found in tree breeding trial data. Trial individuals are related and a degree of correlation is expected between individuals over sites, which can lead to collinearity in the data which may lead to instability in certain selection models. A high degree of collinearity may cause problems and adversely affect the prediction of the breeding values in a BLUP selection index. Simulation studies have highlighted that instability is a concern and needs to be investigated in experimental data. The occurrence of instability, relating to collinearity, in BLUP of tree breeding data and possible methods to deal with it were investigated in this study. Case study data from 39 forestry breeding trials (three generations) of *Eucalyptus grandis* and 20 trials of *Pinus patula* (two generations) were used. A series of BLUP predictions (rankings) using three selection traits and 10 economic weighting sets were made. Backward and forward prediction models with three different matrix inversion techniques (singular value decomposition, Gaussian elimination - partial and full pivoting) and an adapted ridge regression technique were used in calculating BLUP indices. A Delphi and Clipper version of the same BLUP programme which run with different computational numerical precision were used and compared. Predicted breeding values (forward prediction) were determined in the F_1 and F_2 *E. grandis* trials and F_1 *P. patula* trials and realised breeding performance (backward prediction) was determined in the F_2 and F_3 *E. grandis* trials and F_2 *P. patula* trials. The accuracy (correlation between the predicted breeding values and realised breeding performance) was estimated in order to assess the efficiency of the predictions and evaluate the different matrix inversion methods. The magnitude of the accuracy (correlations) was found to mostly be of acceptable magnitude when compared to the heritability of the compound weighted trait in the F_1F_2 *E. grandis* scenarios. Realised genetic gains were also calculated for each method used. Instability was observed in both *E. grandis* and *P. patula* breeding data in the study, and this may cause a significant loss in realised genetic gains. Instability can be identified

by examining the matrix calculated from the product of the phenotypic covariance matrix with its inverse, for deviations from the expected identity pattern. Results of this study indicate that it may not always be optimal to use a higher numerical precision programme when there is collinearity in the data and instability in the matrix calculations. In some cases, where there is a large amount of collinearity, the use of a higher precision programme for BLUP calculations can significantly increase or decrease the accuracy of the rankings. The different matrix inversion techniques particularly SVD and adapted ridge regression did not perform much better than the full pivoting technique. The study found that it is beneficial to use the full pivoting Gaussian elimination matrix inversion technique in preference to the partial pivoting Gaussian elimination matrix inversion technique for both high and lower numerical precision programmes.

NOMENCLATURE AND ABBREVIATIONS

ANOVA	Analysis of variance
BLP	Best Linear Prediction
BLUP	Best Linear Unbiased Prediction
DBH	Diameter at Breast Height
RCB	Randomized Complete Block experimental design
P_0	Parental or first generation of breeding
F_1	Second generation of breeding
F_2	Third generation of breeding
F_3	Fourth generation of breeding
h^2	Narrow-sense heritability
σ_a^2	Additive genetic variance
σ_p^2	Phenotypic variance
σ_f^2	Family component of variance

DEFINITIONS

Backward prediction	Prediction of breeding values of parents based on the performance of their progeny.
Breeding value	The breeding value of an individual is an estimation of the genetic worth of an individual and sometimes defined as twice its General Combining Ability (GCA). In this study breeding values were estimated using BLUP.
General Combining Ability (GCA)	GCA is the average performance of progeny from a particular parent when mated to a number of other individuals in the population and is expressed as a deviation from the average performance of all trees growing in the test.
Family	A family consists of genotypes which were raised from the seed from a single tree.
Forward prediction	Prediction of an individual's breeding values based on their own performance and the family mean performance.
Half-sibs	Group of trees in a family which have one parent in common, usually as a result of open pollination.
Realised breeding performance	In this study the realised breeding performance refers to the breeding values obtained from the backward prediction runs of the relevant combined progeny trial series.

CHAPTER 1
INTRODUCTION

1.1 A brief history of selection index

The genetic improvement of plants and animals through artificial selection in breeding programmes relies on the ability to rank the performance of individuals effectively. In most breeding programmes breeders use phenotypic data obtained in breeding trials to rank the performance of the parents or progeny on pre-selected performance criteria. Through this ranking the best candidates are identified and selected for breeding or production purposes. A number of different selection methods have been developed to identify superior individuals. One approach that has been developed is the use of a selection index. The aim of index selection is to combine all the information from individuals, their parents, full-sibs and half-sibs and potentially also from other relatives into a single index value which is then used to select candidates (Falconer 1989; Mrode 1996). Hazel and Lush (1942) as well as Young (1961 cited in Baker 1986) have shown that the selection index is the most efficient method when compared to other methods such as tandem selection and independent culling. The most efficient method was described as the one that would result in the maximum genetic improvement for the amount of time and effort spent (Hazel & Lush 1942).

The development of the concept of a selection index was based on a discriminate function that was used to differentiate species in taxonomy, developed in 1936 by Fischer (Lin 1978). Smith (1936) took this concept and developed an index specifically for plants (Lin 1978). Smith was one of the first to propose using selection indices for the simultaneous improvement of a number of traits in a breeding programme (Baker 1986). Baker (1986 p2) states that 'Smith introduced the concept that the genotypic worth of a plant could be expressed as a linear function of the genotypic values of several traits'. Smith (1936) also showed that the optimal index coefficients would be those that gave the greatest correlation between the index and the true genetic worth of the individuals (Lin 1978). Selection index, widely used to genetically improve

populations, is the most efficient technique if genetic change is related linearly to economic value (Saxton 1986).

The selection index procedure was further extended by Hazel in 1943 to allow for the selection of individuals in animal populations. Hazel (1943) defined a method to estimate the genetic variances and covariances that were required to derive the index. He also defined the aggregate genotype as being a linear combination of genetic values each weighted by the relative economic value or importance for a trait. The modified equation developed by Hazel is referred to as the Smith-Hazel index and predicts the genetic worth or breeding value of individuals by using regression technology and various sources of information such as economic values, different traits and information from relatives (Lin 1978). In tree breeding the aim of this index is to maximise indirect gain in genetic worth as the breeding values are unknown and only the phenotypic values are known for each tree (Cotterill & Dean 1990). This index assumes that there are equal amounts of data and the same quality of information for all candidates (Hazel 1943). This requirement for balanced data is, however, often not met as field populations usually have individuals that have different levels and sources of data which results in the data being unbalanced (Knott *et al.* 1995; Kerr 1998). Further refinement of the technique was thus required.

Best Linear Prediction (BLP) was an adaptation of the Smith-Hazel Index to accommodate cases of unbalanced or messy data. Best Linear Prediction (BLP) and Best Linear Unbiased Prediction (BLUP) were initially developed for predicting breeding values of dairy cows (Henderson 1963; 1973; 1975 a, b). These techniques are well-suited to predicting genetic or breeding values from data that comes from a wide range of sources, qualities, quantities and ages and are particularly useful when it comes to unbalanced or messy data (White & Hodge 1989; Furlani *et al.* 2005; Postma 2006). For a balanced data set the solutions obtained for Smith-Hazel Index and those for BLP should be the same (White & Hodge 1989). In recent times this type of index selection has increasingly gained popularity in tree breeding, in part due to the need to analyse breeding populations that have moved into advanced generations (Kerr 1998). BLP and BLUP regard breeding values as random effects to be predicted as opposed to fixed effects to be estimated (Henderson 1963; Henderson 1984; Henderson 1973, 1977 cited

in White & Hodge 1988). Hill (1984) and Garrick and Van Vleck, (1987) (cited in White & Hodge 1988) also note that BLP and BLUP methods in most animal breeding applications assume that there are homogenous genetic and error variances.

A potential problem that may adversely affect the effectiveness of selection using BLP or BLUP is the presence of collinearity in the models (Verryn 1994). This problem is of particular relevance in forestry due to the nature of forestry trials. Breeding field trials in the forestry sector are usually established over a number of years and locations in order to sample a wide range of environmental conditions (White & Hodge 1989). There is frequently a large amount of unbalanced or messy data from the breeding trials due to the large numbers of families used and differing survivals (White & Hodge 1989). As these individuals are related, it is expected that there will be a degree of correlation between them, which can lead to collinearity in certain selection models. Because forestry tree breeding trials often comprise of families in multiple trials, this may lead to the inclusion of different sources of family information which is highly correlated, where models are designed to weight family information according to the site parameters (heritabilities and frequencies).

This problem was studied in the simulation research undertaken by Verryn (1994). In the study various predictive techniques were used in 60 randomly generated breeding populations of 1000 trees. BLP was not obtaining the predicted gains in 80% of the cases studied and these cases where instability may be present were a point of concern. Possible explanations for the under-performance of BLP and instability in these studies included the impact of collinearity (Verryn, 1994; Verryn & Roux 1998). This study revealed the need to investigate the effects of collinearity leading to instability and possible better solutions in real data.

1.2 Collinearity and its effects

A number of different definitions have been attached to the term of collinearity. Some authors (e.g. Weisberg 1980) distinguish between the terms collinearity and multicollinearity whereas other authors use either one or the other term. Here the

convention of Belsey *et al.* (1980) will be followed who suggested that the term multicollinearity is redundant and that the term collinearity be used exclusively.

Collinearity has been described as an 'approximate' linear relationship or shared variance among the predictor variables in the data (Belsey *et al*. 1980). Collinearity in the regression context exists when there is an exact or nearly exact linear relationship among two or more of the input variables (Hocking & Pendleton 1983). Collinearity or ill-conditioning has also been described as a problem that arises when there are highly correlated independent variables (Mason 1987) or correlated covariates (Zuur *et al.* 2010). Regression models containing such variables may give unstable parameter estimates because small changes in the observed values of the dependent variables could lead to large changes in regression coefficient estimates (McGriffin *et al*. 1988). Collinearity may therefore also present a problem in BLUP where linear regression models may be used to predict the variances and covariances (second moments) needed for the BLUP model calculations (White & Hodge 1989). Collinearity is not uncommon in tree breeding trials and BL(U)P models. In tree breeding practice, the second moment matrices are seldom known constants and are therefore estimated and instability symptoms are often detected (Verryn & Roux 1998).

Collinearity results in regression coefficients with round off errors, unstable estimates, unexpected signs (e.g. a variable may have a negative instead of the expected positive effect on the response variable) and inflated variances (McGriffin *et al*. 1988). Verryn and Roux (1998) refer to instability in breeding as being associated with cases when one or more of the β-coefficients of the solution vector (b-vector) in BL(U)P are disproportionately large or small or have the incorrect sign (either positive when it should be negative or vice versa).

It is difficult to determine in which cases the degree of collinearity in the data becomes damaging (Mason & Perreault 1991) as many models do include correlations. According to Mason and Perreault (1991) there has not been much research into systematically identifying the detrimental effects of various degrees of collinearity (on its own and in combination with other factors). Others such as Farrar and Glauber (1967) suggest that the difficulties associated with a data set that has collinearity will

depend on the severity of that problem. If the input variables for a regression are not correlated, the contribution of the individual variables will be additive and their relative importance can be considered, but when they depart from orthogonality, the role of individual variables is less clear and various selection methods may give conflicting results (Hocking & Pendleton 1983). Hocking and Pendleton (1983) suggest that variable selection should take place in the concluding stages of analysis when the data has been cleaned up and the researcher has a better understanding of the role of the input variables in describing the response.

It is important to consider the collinearity in data, especially when regression analysis is being used because of the various, potentially undesirable consequences (McGriffin *et al*. 1988; Mason & Perreault 1991). Although collinear predictors may adversely affect the variance of a specific coefficient, the collinearity effect does not operate in isolation (Mason & Perreault, 1991). The effects of factors such as sample size and overall fit of the regression models and the interactions between these factors and collinearity play a role in the adverse effects on the coefficient (Mason & Perreault 1991). If a data set has enough collinearity to cause computations to be inaccurate then it should be considered to be ill-conditioned (Leath & Carroll 1985). In some cases collinearity may result when several independent variables are very weakly correlated and their interrelationships are not as obvious (McGriffin *et al*. 1988). Rook *et al*. (1990a) looked at the effects of collinearity in the prediction of voluntary intake of grass silage by beef cattle and showed that collinearity among independent variables may lead to unstable estimates of regression coefficients. They found that these estimates may change markedly when there are small changes in the estimation data and lead to poor prediction in the independent data sets.

De Carvalho *et al*. (1999) showed that the classic selection index (proposed by Smith (1936) and Hazel (1943)), under collinearity, did not give simultaneous gains in wheat grain production and its main components due to instability and therefore low precision of the coefficient index estimates. In classic selection index, where the coefficient vector is a function of the inverse of the phenotypic variance covariance matrix, if perfect collinearity exists, the phenotypic matrix will be singular and a unique inverse non-existent (De Carvalho *et al*. 1999). This case rarely occurs, however, as the

phenotypic matrix nears singularity the corresponding index will become less reliable (De Carvalho *et al*. 1999). An explanation is that the variance associated with the index coefficients becomes larger as the phenotypic matrix nears singularity (De Carvalho *et al*. 1999).

In 1982, Mandel, recognised that collinearity is one of the largest problems that may be encountered in many data sets when least-squares techniques are used (McGriffin *et al*. 1988). In a predictive model, collinearity is a concern as future prediction errors may occur unless the relationships that are present in the collinear set of data used to estimate the regression coefficients remain fixed in the future data sets (Bare & Hann 1981).

Mitchell-Olds and Shaw (1987) investigate the fitness-regression approach used by Lande and Arnolde (1983) which was a method that employed multiple regression of relative fitness on the observed characters on an individual's fitness, and note that collinearity can be problematic for the analysis and interpretation thereof. When there is perfect intercorrelation between characters included in the analysis then the phenotypic variance-covariance matrix becomes singular and its inverse cannot be computed uniquely resulting in the inability to calculate the estimates of β from the full set of data (Mitchell-Olds & Shaw 1987). Mitchell-Olds and Shaw (1987) state that when inverting a matrix that is nearly singular the solution is computationally unstable, with different matrix inversion methods yielding different results, and the instability is reflected in large sampling variances of the estimates of β.

1.3 Detecting collinearity or diagnostics for collinearity

Collinearity is a problem that is not always tested for or treated by field biologists and statistical packages and diagnostics to deal with collinearity were only developed in the early 1980s (McGriffin *et al*. 1988). An amount of subjective judgment is needed to make a decision as to what levels of correlation among variables or values of variance inflation factors (VIFs) of estimates actually represents collinearity problems (McGriffin *et al*. 1988).

There are numerous ways of detecting collinearity ranging from simple rules of thumb to complex indices (Belsey *et al*. 1980; Mason & Perreault 1991). Some of these include examining the correlation matrix R of the predictor variables or its inverse R^{-1}, calculating the coefficients of determination, R^2 of each dependent variable regressed on the remaining predictor variables, and measures that are based on the Eigen structure of the data matrix X, which include variance inflation factors (VIF), trace of the $(X'X)^{-1}$ and use of the condition number or condition index and variance-decomposition proportions (VDP) associated with the eigenvalues (Belsey *et al*. 1980; Mason & Perreault 1991; Roso *et al*. 2005). Various authors refer to the variance inflation factors (VIF) as the diagonal elements of the inverse of the correlation matrix (Marquardt 1970 cited in Hocking & Pendleton 1983; Rook *et al*. 1990a; Roso *et al*. 2005). None of the approaches have been fully successful at diagnosing the presence or assessing the potential harm of collinearity (Belsey *et al*. 1980).

VIF is one of the most common measures of collinearity and for ordinary least squares (OLS) this factor indicates the inflation in variance of each regression coefficient compared to a case of orthogonality (Roso *et al*. 2005). Chatterjee *et al*. (2000 cited in Roso *et al*. 2005) suggest that values of VIF that are larger than 10 could indicate that collinearity is causing problems in estimate calculations. Rook *et al*. (1990a) also suggest that when the VIF is in excess of 10, it indicates severe collinearity leading to unstable estimates of associated least-squares regression coefficients.

The Condition Index (CI) is calculated using the square root of the division of the largest eigenvalues and each of the eigenvalues elements of the correlation matrix. Large CI values of above 30 are suggested to indicate the presence of collinearity (Belsey 1991 cited in Roso *et al*. 2005). A large CI is obtained when there are a number of small eigenvalues and therefore a small resultant determinant which indicates collinearity (Roso *et al*. 2005).

Variance-decomposition proportions (VDP) is a statistic that indicates which variables are involved in linear dependencies and how much of the variance of the parameter estimate is associated with each of the eigenvalues (Roso *et al*. 2005). Testing for the degree of collinearity (or first indication thereof) may also be executed by pairwise correlation coefficients between all the independent variables in the data sets (Rook *et al*. 1990a).

Detailed discussion of the formulas for the detection techniques are discussed in Belsey *et al*. (1980) and Roso *et al*. (2005).

1.4 Methods of handling or coping with collinearity and resulting instability

Studies have been carried out by various authors to find alternative techniques to handling instability as a result of collinearity. These techniques include principal components analysis, ridge regression and solutions based on ridge regression (Hoerl & Kennard, 1970a, b; Vinod 1978; Bare & Hann 1981; Newell & Lee 1981; Leath & Carroll 1985; McGriffin *et al*. 1988; Rook *et al*. 1990a, b; Verryn 1994; De Carvalho *et al*. 1999), bending (Saxton 1986) and simple genetic algorithm solutions (Verryn *et al*. 1995). Often when there is collinearity among the independent variables in a regression model, variables are deleted in order to continue with a sensible hypothesis test (Morzuch & Ruark 1991).

Rook *et al*. (1990a) made use of various techniques in the analysis of their data of the voluntary intake of grass silage by beef cattle, such as principal components analysis, linear functions of original variables, ridge regression and models that used fewer original variables to address the problems of collinearity. They found these methods effective in removing collinearity and showed that they provide a good alternative to the normal use of least-squares models and should show better performance as predictive models.

1.4.1 Principal components regression

The effects of collinearity on parameter estimates can be directly quantified in terms of principal components by using condition indices (CI) and variance decomposition proportions (the percentage of variability in parameter estimates caused by a certain principal component) (McGriffin *et al*. 1988). Moderate collinearity problems are shown by CI > 70 and CI > 100 is indicative of severe collinearity problems (McGriffin *et al*. 1988). Belsey *et al*. (1980) proposed that when a principal component has a CI > 30 and a variance decomposition proportion that is greater than 50% for two or more regression coefficients then it represents a collinearity problem that should be dealt with.

According to Rook *et al*. (1990a) principal components are a set of variables that are linear functions of the original variables and are orthogonal to each other. This technique places restrictions on the independent variables by orthogonalizing them and then only retaining those dimensions of the transformed data that account for most of the variability in the independent variables (Morzuch & Ruark 1991). The principal component that provides the least amount of explanatory power for the model being used can be considered as a candidate for deletion (Morzuch & Ruark 1991).

Collinearity may be considered to be present when a latent root is close to zero i.e. an approximate linear dependence exists between the original variables (Rook *et al*. 1990a). In this way the original variables that are likely to cause severe collinearity problems can be identified. By removing the principal component that gives rise to collinearity by excluding it from the regression (setting its coefficient to zero) the collinearity is removed (Rook *et al*. 1990a). The estimates of regression coefficients will be biased, but their signs and magnitude should be more stable and in line with the theoretical expectations (Rook *et al*. 1990a).

According to Morzuch and Ruark (1991) the advantage of principal components procedure is that it does not eliminate any of the structural independent variables when dealing with the collinearity. Those components that account for most of the variability in the model are considered to be important and are kept in the model. Also size of the

eigenvalues is used to benchmark importance of components (Morzuch & Ruark 1991). By taking a subsample from their known data set in order to create more collinearity problems, Morzuch and Ruark (1991) showed that the principal component technique leads to less model specification bias than a stepwise variable selection technique.

Collinear variables are often obvious in tree breeding data, for example when different site means of the same set of families is included or when using repeated measurements at different ages as different traits and therefore the application of principal components to change the model specification may not be as high a priority in forestry as in other modelling environments (Verryn 1994).

Examples of the use of principal component analysis for the treatment of collinearity include a study by Morzuch and Ruark (1991), where principal components regression was used to deal with collinearity in tree growth data as well as a study by Rook *et al*. (1990a) who used principal components regression to identify and eliminate collinearity from the independent variables in their data of the voluntary intake of grass silage by beef cattle.

1.4.2 Ridge regression

Ridge regression was first suggested by Hoerl in 1962 to control general instability associated with least squares estimates (Hoerl & Kennard 1970a). The method is explained in detail in Hoerl and Kennard (1970a). The method involves the addition of a small constant value, k (k>0), to the diagonal elements of the correlation matrix and the solving as usual for the regression coefficients (Bare & Hann 1981). The constant is added to the diagonal of the X'X matrix after it has been standardized but before the inversion of the matrix (Leath & Carroll 1985). The resulting ridge coefficient is a biased estimate which may have decreased variances, but these can decrease more rapidly than the bias increases and thus the choice for data with a large amount of collinearity is between small bias, k, or large variance (Leath & Carroll 1985). The choice of a k value must take into account the balance between bias and variance (Weisberg 1980). When the constant value is zero then the result is the same as Ordinary Least Squares (OLS) estimates. The k values usually lie between zero and one

but may have any positive value. The larger the value the larger the bias will be (Weisberg 1980; Bare & Hann 1981). By the adding of k to the diagonal of X'X matrix product the size of the eigenvalues of the matrix are increased and this may correspond to a decrease in the distance between β and the estimate of β which will be small (Leath & Carroll 1985). According to Hoerl and Kennard (1970b) in ridge regression variable selection is unique because the variables are selected on the basis of trends shown by the ridge trace of the coefficients versus k, allowing for a subjective selection based on mathematical criteria.

Ridge regression sacrifices unbiasedness in order to obtain parameter estimates that have a smaller mean square error than that of unbiased methods of ordinary least squares (OLS) (Bare & Hann 1981). Hoerl and Kennard (1970a, b), show that there is a k value (positive) that results in the mean square error of the ridge estimator being less than that of the OLS estimator. There is always a ridge estimate that will give a smaller mean square error than for the least squares solution solutions (De Carvalho *et al*. 1999). Ridge regression also results in a decrease in standard error of the estimate of the coefficient (Bare & Hann 1981). In the study of Leath and Carroll (1985) instability of coefficients was demonstrated by large changes in the vector of estimated ridge coefficients, $\hat{\beta}^*$ of Hoerl and Kennard (1970a), with only small changes in the k constant. Ridge regression should be considered when there is a high degree of collinearity in the data (Leath & Carroll 1985). Marquardt and Snee (1975) suggest that ridge techniques should be used only after nonessential ill-conditioning has been removed by means of standardizing the data (Leath & Carroll 1985). Removing collinearity, by methods such as standardization, is important as collinearity among variables could be the main cause of instability in multifactor loss prediction models as used by Leath and Carroll (1985).

Bare and Hann (1981) discussed the applications of ridge regression in the forestry context. They emphasized the importance of the concerns regarding the degree of collinearity whether the regression equation is used for prediction purposes or for creating a descriptive model. When developing a predictive model the main objective is to select those variables that lead to the minimization of the mean square error of prediction (Chatterjee & Price 1977 cited in Bare & Hann 1981). In a study conducted

on independent data, Rook *et al*. (1990b) found that ridge models were superior to other models such as ordinary least-squares linear regression and principal component regression even in those cases where there was little collinearity among the independent variables.

Two problems exist when using ridge regression. One is that if the true least squares population parameters are unknown then the amount of bias that is introduced will be unknown (Bare & Hann 1981). Hoerl and Kennard (1970a) state that a k>0 exists that although introducing some bias, will substantially reduce the variance and thereby improve the mean square error of estimation and prediction. The other problem is to determine the best k value for a specific problem. Various methods have been suggested for the suitable choice of k value. According to Gruber (1998 cited in Roso *et al*. 2005) there are many different methods that have been proposed for selecting an appropriate k value, however, there is no consensus on which of the methods is the most satisfactory. In general the selection of an appropriate k will depend on the data and on the model used (Roso *et al*. 2005).

Hoerl and Kennard (1970a) suggested a method they call the ridge trace, which is a plot of all the standardized regression coefficients over a range of k values. In addition the authors suggest a number of different indicators that can serve as a guide to the best choice of k value:

(a) the ridge trace will stabilize at a particular value of k and exhibit the general characteristics of an orthogonal system

(b) coefficients will not have unreasonable absolute values "with respect to the factors for which they represent rates of change"

(c) coefficients that appeared to have an incorrect sign at k=0 will have changed and have the correct sign

(d) inflation of the residual sum of squares will not be unreasonable and it will not be large relative to the minimum value or large relative to a reasonable variance that would be expected for the data processing.

Bare and Hann (1981) caution that these guidelines involve a substantial amount of subjectivity in their use in actual situations.

Various authors have suggested examining the VIF as a function of the ridge estimator or parameter (k) (Chatterjee & Price 1977 and Neter *et al*. 1983 cited in Delaney & Chatterjee 1986). When the ridge parameter is zero, large VIF values indicate that there is severe collinearity in the data (Delaney & Chatterjee 1986). This method was proposed by Marquardt (1970) who suggests a k value is to be used that will give a maximum VIF of between 10 and one, with a VIF closer to one being more preferable (Bare & Hann 1981). When there are perfect orthogonal conditions the VIFs are all equal to one, however under perfect collinear conditions one or more of the VIFs will tend towards infinity (Bare & Hann 1981). The k value needs to be nonstochastic in order for the equations for the expectation and covariance of the ridge estimators that Hoerl and Kennard (1970a) developed to remain valid (Bare & Hann 1981). The VIFs will, however, not all be close to one at the same time which poses a problem and makes the choice of an exact k difficult (Delaney & Chatterjee 1986).

The determinant of the correlation matrix has also been proposed to be used as a criterion for choosing k values (Farrar & Glauber 1967). A determinant is calculated for each k value and values close to zero indicating a high degree of collinearity and values close to one indicating low collinearity (Bare & Hann 1981).

Verryn *et al*. (1995) adapted the ridge regression techniques from Hoerl and Kennard (1970a) and the Simple Genetic Algorithms of Goldberg (1989) to obtain models for prediction. The authors used simulation to automate and test these processes. A simulated genetic (breeding) population was used and relative performances of iterative solutions with a range of k values were compared to the true solution in the stochastic population (Verryn *et al*. 1995).

Leath and Carroll (1985) studied the yield reduction in soybean cultivars in response to infection by *Fusarium oxysporum*. They predicted the yield reduction using an ordinary least squares model (selected by stepwise procedure) and a ridge regression model. The authors found that their ridge prediction model was more stable than the OLS model and most of the collinearity was handled effectively.

Newell and Lee (1981) used ridge regression as an alternative to multiple linear regression (MLR) in food technology data where there is often a problem with highly correlated data. They show that ridge regression is a suitable alternative to MLR in their data set to overcome the problem of unstable estimates and inflated variances.

De Carvalho *et al*. (1999) adapted the ridge regression method to classic selection index in their study and found that the ridge index gave more viable index coefficient estimates as well as gains for the characters under study.

Ngo *et al*. (2004) observed the performance of ridge regression compared to OLS in engineering models. Studying imperfect models and comparing a large data set and a smaller data set drawn from the larger one, the authors found that prediction using ridge regression performed better than OLS and in addition, surprisingly in the smaller data set compared to the larger one.

Roso *et al*. (2005) analysed pre-weaning weight gains of beef calves, estimating genetic effects in this data in which collinearity occurred. They looked at the degree and the nature of the collinearity and used ridge regression methods as an alternative to ordinary least squares (OLS) and found that ridge regression performed better than the least squares estimator with regard to mean squared error of predictions (MSEP) and variance inflation factors (VIFs).

Delaney and Chatterjee (1986) combined the concepts of bootstrap and cross-validation methods to obtain an optimal choice of ridge parameter based on the minimum mean square error of predictions (MSEP). They used a Monte Carlo simulation study to evaluate the performance of the bootstrap choice of ridge parameter and performance measures included mean square error (MSE) and MSEP. Delaney and Chatterjee (1986) included simulation via singular value decomposition (SVD) of the design matrices with varying degrees of collinearity. SVD was used to generate design matrices with condition numbers of two, five, 10, 50 and 100 in their study. The condition number is the ratio of the maximum singular value and the minimum singular value in the SVD technique (Delaney & Chatterjee 1986). The condition number interpretation suggested by Belsey *et al*. (1980) was that numbers between five and 10

indicate weak dependencies among the columns of the design matrix and those greater than 30 indicate strong dependencies. When the condition numbers exceed 100 it can cause significant variance inflation and degradation of the regression estimates (Belsey *et al*. 1980).

1.4.3 Bending

A method called bending was suggested by Hayes and Hill (1981 cited in Saxton 1986) which introduces bias into the estimation procedure to obtain index weights that are closer to the true values. Bending is similar to ridge regression (Saxton 1986). Saxton (1986) compared the methods in a simulation experiment and used two properties to compare the methods, (1) the average fraction of possible genetic response achieved and (2) the percentage of experiments where the modified index gave as much response as the usual least squares index. Both ridge index and bending index gave better gains than the usual index. Both ridge and bending reduce the spread in the eigenvalues of the product of the inverse phenotypic variance covariance matrix with the genotypic variance covariance matrix (Saxton 1986). For large population sizes bending and ridge index gave similar results. Saxton (1986) notes that one main disadvantage of the bending method is the selection of the bending parameter.

Model simplification methods such as elimination of variables which do not contribute significantly to the model (Morzuch & Ruark 1991; Verryn 1994), averaging collinear variables into one effect instead of having them as separate effects (Mitchell-Olds & Shaw 1987) and principal components regression may not always provide the best solution to problems of collinearity. This is especially the case when there are multiple sites and multiple traits in the model. Instability may not occur in all families or at all sites and decisions on how to and when to simplify the model may be complicated. The power of BLUP may be lost in such cases and the process is likely to be time and computationally intensive.

Models which have variance estimates for each site and which therefore weight the effects of family means optimally are rather used in this study.

The different alternatives to coping with collinearity may lead to very different conclusions and what may be gained from the different alternatives is often unclear (Mason & Perreault, 1991). Mason and Perreault (1991) attribute this ambiguity with the inadequate knowledge about what degree of collinearity may be considered to be harmful and that data with extreme levels of collinearity are rare whereas more modest degrees of collinearity in data is more common.

1.5 Objective of the study

BLUP is widely used for selection in forestry trials but despite the fact that collinearity is likely to be encountered in the data, the effect that collinearity and resulting instability has on the efficiency of the predictions is not yet known. Although studies using simulations have indicated potential problems in predicting performance and the subsequent effect on genetic gains, no studies based on forestry field data have been reported to date. The objective of this study was therefore to investigate the potential problems associated with collinearity in tree breeding data and instability in the BLUP selection estimates from such data. The study was carried out to obtain insight into the problem of collinearity in forestry trial data.

As a case study, data from a number of forestry breeding trials of pure species *Eucalyptus grandis* and *Pinus patula* were used which included material from three generations of breeding in *E. grandis* and two generations of breeding in *P. patula*.

The objective was addressed by investigating the following:

- Comparisons of different matrix inversion techniques within the BLUP selection index calculations to assess whether there was any difference in their effectiveness in dealing with data which has a degree of collinearity.
    - Three matrix inversion techniques, singular value decomposition (SVD), Gaussian elimination with partial pivoting and Gaussian elimination with full pivoting, were used.
    - An adapted ridge regression technique was also used and compared.

- Comparison of a Delphi and a Clipper version of the same BLUP selection index programme, which run at different computational numerical precisions, was also carried out.
- Accuracy (correlations) of predictions of individuals from one generation with the realised breeding performance of the families in the next generation.
- Realised genetic gains comparison.

CHAPTER 2
MATERIALS

2.1 Introduction

Historical data from 39 *Eucalyptus grandis* Hill ex Maiden and 20 *Pinus patula* Schiede et Deppe in Schlechtendal et Chamisso breeding trials were used in this study to investigate the effects of collinearity in forestry field data and various methods of remedial treatment of instability caused by collinearity in BLUP selection solutions. The main advantage of using this historical data was that three generations of data was immediately available without the expense of trial establishment and an extended waiting period for the forestry field trials to be at a suitable age for trait measurements. In addition, this study required data from trials from succeeding generations for which historical trials were the best available option. The disadvantage of using historical data is the lack of control over factors such as trial design, choice of controls, trial size, assessment traits and age of assessments available for use in the study.

This study was carried out to investigate the effectiveness of different matrix inversion techniques and an adapted ridge regression technique in dealing with collinearity during the calculation of BLUP estimates. The research strategy is outlined in Figure 2.1 (*E. grandis*) and Figure 2.2 (*P. patula*) (similar approaches have been used by others for example Sasaki (1992) in animal breeding and Postma (2006) in natural selection populations). Trial data from two species was selected to represent the performance of parents and their progeny. The trials were established in multiple trials/sites and some over multiple locations. For *E. grandis* a series of forward BLUPs (rankings) using various traits and economic weightings of historic F_1 *E. grandis* data were made. These predictions were then compared with the 'realised' rankings (backward predictions) of F_2 *E. grandis* data using the same selection traits and economic weights. The efficiency of various analytical methods used in the BLUP predictions were compared (F_1F_2 scenario). The F_2 data was also used for forward selection BLUPs and these predictions compared with the 'realised' rankings of F_3 *E. grandis* data (F_2F_3 scenario). The backward predictions were regarded as the best available empirical measure of the

realised breeding values (genetic gains) of the open-pollinated F_1 and F_2 parents. Realised genetic gains were also calculated for the F_1F_2 and F_2F_3 scenarios and the gains from the different methods used for BLUP calculations were compared. The same process was followed with F_1 and F_2 *P. patula* historic data and is illustrated in Figure 2.2.

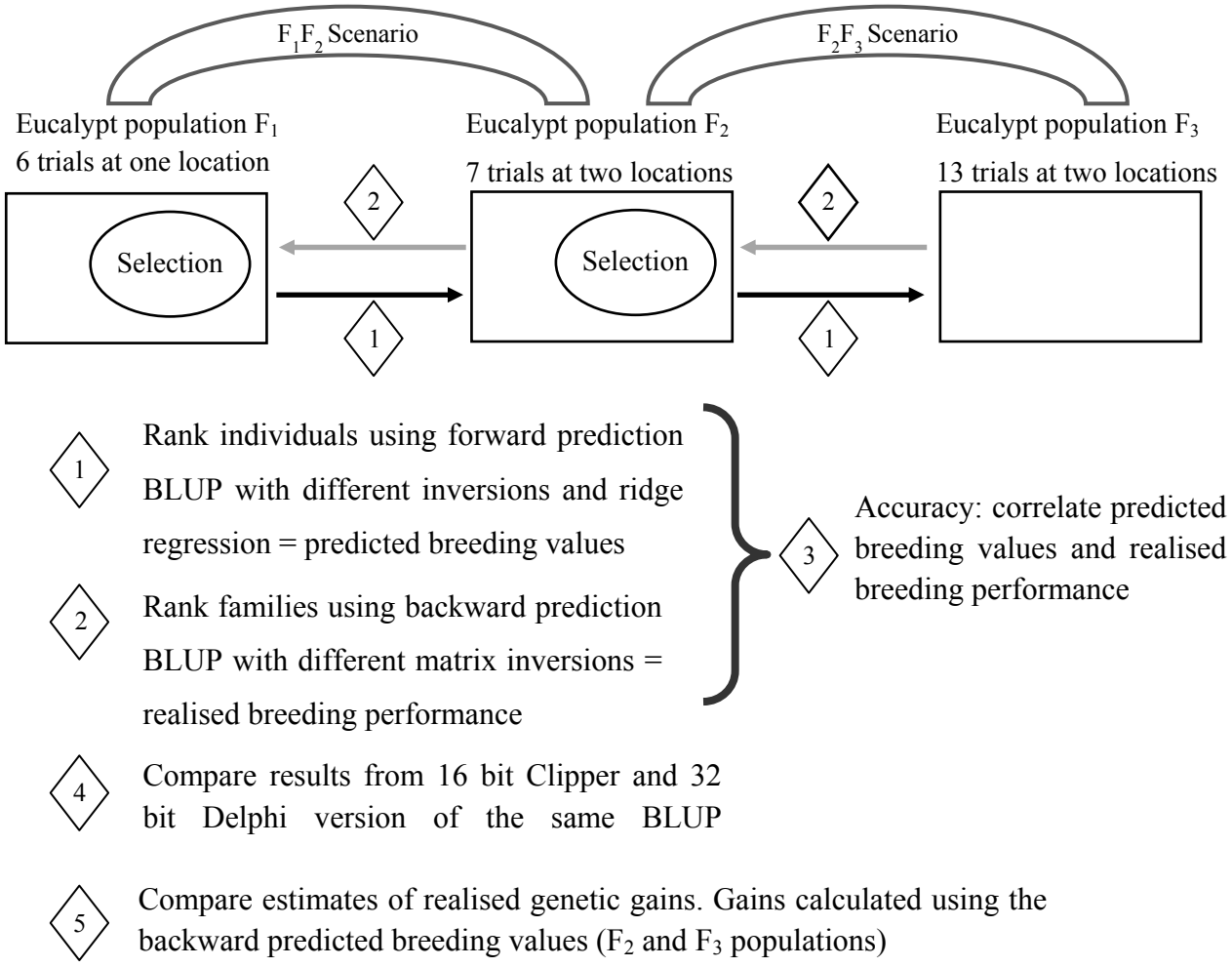

Figure 2.1 Research strategy to investigate collinearity in *E. grandis* forestry field data.

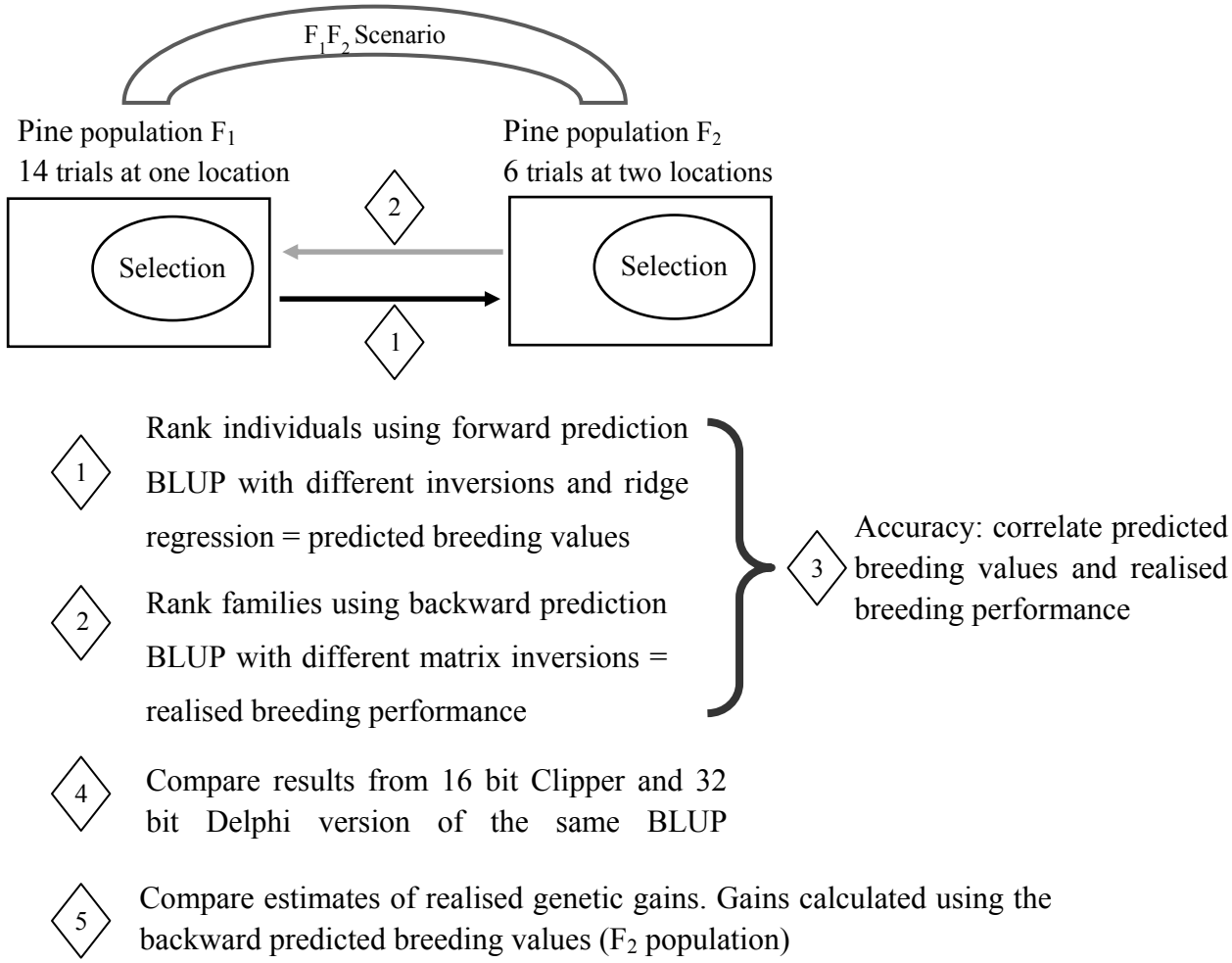

Figure 2.2 Research strategy to investigate collinearity in *P. patula* forestry field data.

2.2 Criteria for selection of data

Suitable experimental data for the study had to meet the following requirements:

- **Suitable trials:** This study required sets of trials for each species that represented populations at different generations of breeding. Records of the selections (pedigree) that were made in each generation to form the next generation of breeding trials were needed.
- **Suitable traits and assessment ages:** The same traits had to have been assessed in each generation of trials. Trait assessments at similar tree ages was preferable as expression of traits may vary with age (Franklin 1979; Balocchi *et al*. 1993; Xiang *et al*. 2003).

- **Suitable genetic structure of trials:** Sufficient numbers of families and individuals within families was required for sound statistical analysis and for reliable heritability estimates and other genetic estimates required for calculating the BLUP selection indices and genetic gains. Ideally the population data should have at least 75 families and 10 individuals per family (Hettasch et al. 2011).
- **Data with some degree of collinearity:** The study required data that had some degree of collinearity in order to assess the effectiveness of different matrix inversion techniques in handling data with collinearity in the BLUP calculations. Although it could not be known at the outset whether the data had collinearity or not, a possible indication that there could be collinearity in the data is the high correlations between variables (Belsey *et al.* 1980).

2.3 Description of data sets

2.3.1 Broad background and history to the CSIR *Eucalyptus grandis* genetic resource

The South African Forestry Research Institute, SAFRI (which was later transferred to the CSIR) *E. grandis* breeding programme began in 1962 with the phenotypic selection of 689 first generation (P_0) selections (see Figure 2.3 which shows the trials from which the selections for each generation were selected, however, only shows the trials that were used in this study due to limited space in the Figure). Most of these selections (594) were from plantations in the summer rainfall regions of Mpumalanga, Limpopo and KwaZulu-Natal provinces in South Africa (Pierce 1996). The first generation selections were used to establish three diallel, four inbreeding depression trials and one fertilizer by progeny trial in order to gain information on the breeding patterns within *E. grandis* (Pierce 1996).

In the mid 1970s selections were used to establish a series of six progeny trials at the J.D.M. Keet Forestry Research Station in the Limpopo province (see Figure 2.3) and two complementary trials in KwaZulu-Natal province in South Africa (Pierce 1996). These trials had open-pollinated progeny from 99 selections (Pierce 1996). The trials were felled over consecutive years during the early 1980s and 563 selections were made

(see Figure 2.3) and used to establish further second generation open-pollinated progeny trials (Pierce 1996).

During the early 1970s *E. grandis* seedlots were imported from Australia and were used to establish a series of provenance trials in the summer rainfall region. Further imports were made of individual families and bulk provenances during the 1970s and further trials were established. There were a total of 147 provenance families incorporated into 19 trials (Pierce 1996). The gene pool was supplemented during the mid 1980s by further imports of 323 families from 32 provenances and progeny / provenance trials were established. A number of second generation (F_1) selections have been made from the old provenance collections and the newer progeny / provenance trials.

Other infusions into the *E. grandis* breeding programme were made in the late 1970s from the New South Wales (30 families), Florida (300 families) and later the Columbian (90 families) programmes and various progeny trials were established (Pierce 1996). Later, second generation (F_1) selections were made from these trials. All of the progeny trials of local selections were divided and managed as "seedling seed orchards" and two generations were turned over in these orchards. Selections for second and third generation of breeding were made by forward selection in the open-pollinated *E. grandis* breeding population.

All of the old provenance trials, non-South African origin trials and most of the second generation local South Africa trials were analysed and selections made. The open-pollinated seed of the selections was collected and sown and these were then incorporated into a new *E. grandis* breeding F_3 (fourth generation) population through a series of 13 progeny trials (see Figure 2.3) established in Limpopo and KwaZulu-Natal provinces (Pierce 1996).

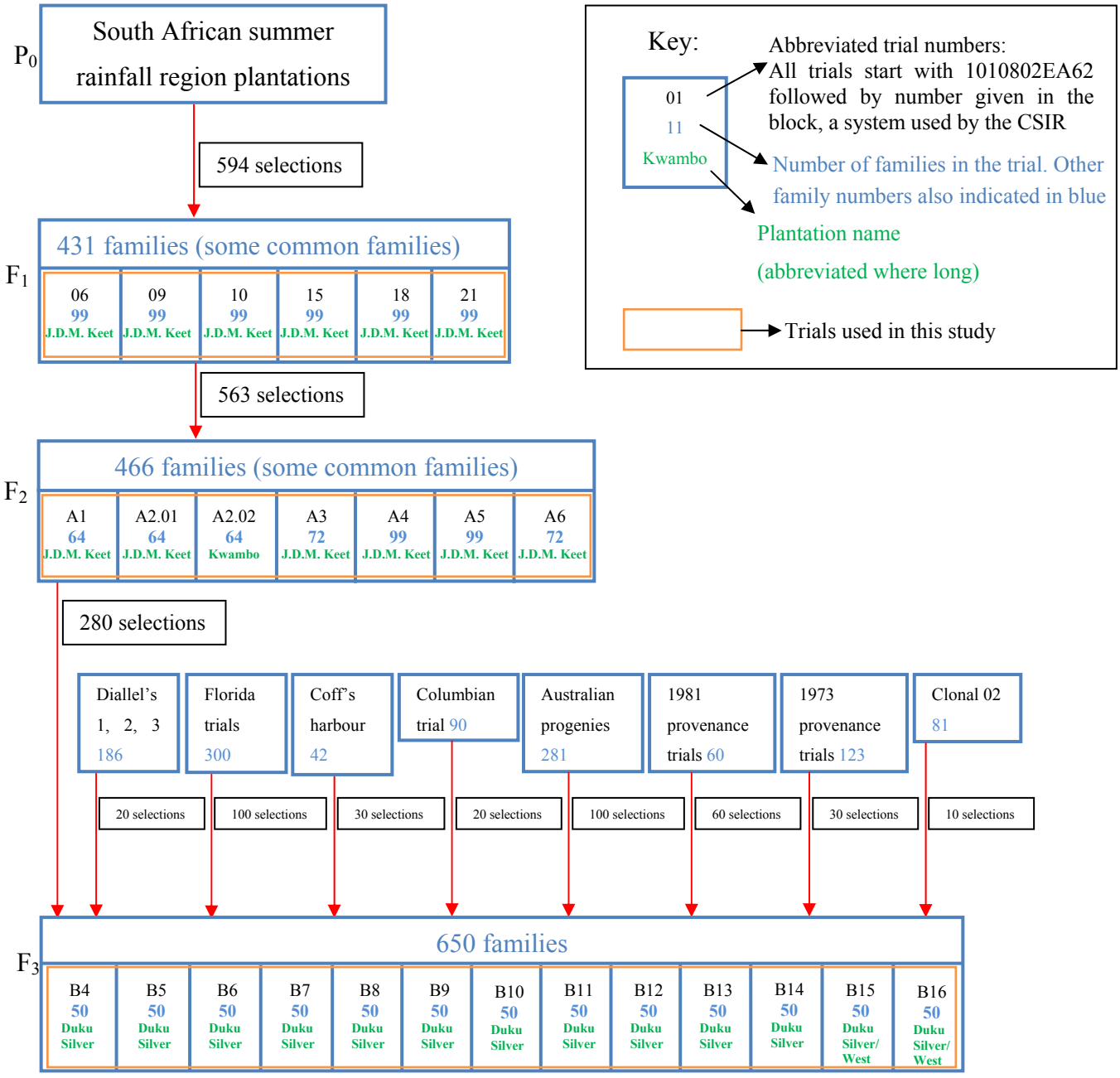

Figure 2.3 *E. grandis* F_1, F_2, and F_3 breeding populations.

2.3.1.1 E. grandis trials and genetic material used in this study

The data used in this study was obtained from the CSIR *E. grandis* breeding programme as described above. Local unimproved seed was collected from 594 P_0 selections (based on a method of visual searching for superior phenotypes – mass selection) made in various unimproved plantations in the summer rainfall region of South Africa in the 1960s. Seed from these P_0 selections was used to plant *E. grandis* F_1 trials which included the progeny tests 1010802EA6206 (EA6206), 1010802EA6209 (EA6209), 1010802EA6210 (EA6210), 101802EA6215 (EA6215), 1010802EA6218 (EA6218) and 1010802EA6221 (EA6221) (as shown in the F_1 block in Figure 2.3) that were used in this study. A total of 431 families were included across these six F_1 trials used in this study. Each of the trials consisted of 99 families (there were some common families across the trials) which were later felled for seed collection and collection of cuttings material after felling, from coppice for production of clones.

The six F_1 trials were all planted in compartments at J.D.M. Keet plantation in Limpopo province between December 1975 and March 1983 (see Table 2.3 for details of these trials).

F_1 selections (563 selections) were made in the F_1 trials based on trial measurements and data analysis at clear felling. The selections from the trials at J.D.M. Keet plantation were made between 1981 and 1989 (Table 2.4) and were used to establish the *E. grandis* F_2 trials which included trials 1010802EA62A1 (A1), 1010802EA62A2.01 (A2.01), 1010802EA62A2.02 (A2.02) (the 1010802EA62A2 trial was duplicated at two sites, see Table 2.4) and 1010802EA62A3 - 1010802EA62A6 (A3, A4, A5 and A6) (as shown in the F_2 block in Figure 2.3). The *E. grandis* F_2 trials consisted of open-pollinated families from F_1 selections selected from trials 1010802EA6206 (for trial A1), 1010802EA6209 (for the two A2 trials, A2.01 and A2.02), 1010802EA6210 (for trial A3), 1010802EA6215 (for trial A4), 1010802EA6218 (for trial A5) 1010802EA6218 (for trial A6). A total of 466 F_2 families were included in the seven A-series trials used in this study and details of the number of families and controls included in each F_2 trial are presented in Table 2.4 and illustrated in Figure 2.3.

Six of the F_2 trials (trials A1, A2.01 and A3 - A6) were planted at J.D.M. Keet plantation in Limpopo province and the second A2 trial (A2.02) trial was planted at KwaMbonambi plantation in KwaZulu-Natal province. The trials at J.D.M. Keet were established between March 1983 and March 1990 and the trial at KwaMbonambi plantation was established in April 1984 (see Table 2.4 for details of these trials).

The selections of superior trees in the many provenance, family trials of provenances, local and imported material progeny trials (including the F_2 trials EA62A1 - EA62A6) took place during 1990 to 1992 and open-pollinated seed was collected from these selections.

The progenies of the families collected between 1990 and 1992 (as mentioned above) were divided into 11 sublines of 50 families per subline in December 1995. The progenies of the families collected in 1997 were also divided into a further two sublines of 50 families each. There were twenty individuals per family in each subline and no common families between sublines. Each of the 13 sublines received an equal representation of randomly allocated parents from local and imported seed sources and were used to establish the *E. grandis* F_3 trials.

E. grandis F_3 trials included the trials 1010802EA62B4 – 1010802EAB16 (as shown in the F_3 block in Figure 2.3) planted as two complete duplicate trial series in Limpopo and KwaZulu-Natal provinces (Table 2.5). A total of 650 open-pollinated (half-sib) families were included in each set of 13 F_3 trials included in this study. The first 11 progeny trials, 1010802EA62B4.01 – 1010802EA62B14.01 (B4.01 – B14.01) were established in May and June 1996 at Dukuduku plantation in KwaZulu-Natal province and the duplicate set of 11 progeny trials, 1010802EA62B4.02 – 1010802EA62B14.02 (B4.02 – B14.02) in May 1996 at Silverfontein plantation in the Limpopo province. The remaining two progeny trials were established in June 1997 at Westfalia plantation in close proximity to Silverfontein plantation, trials 1010802EA62B15.02 and 1010802EA62B16.02 (B15.02 and B16.02) in the Limpopo province. The duplicate trials were planted in August 1997 at Dukuduku plantation (trials 1010802EA62B15.01, B15.01 and 1010802EA62B16.01, B16.01) in the KwaZulu-Natal province. In this study the trial series (11 trials at Silverfontein plantation and two at Westfalia) in

Limpopo (referred to as Silverfontein data from Chapter 4 onwards) and the trial series (13 trials) in KwaZulu-Natal (referred to as Dukuduku data from Chapter 4 onwards) were treated as two data sets as they were two large sets of trials and were geographically separated by a large distance.

The detailed site information for the F_1 trials and the F_2 trial sites are shown in Table 2.1 and the details of the F_3 trial sites are shown in Table 2.2.

At age 30 months the F_2 trials were thinned by 50 % reducing the plots to the best remaining two trees and then at age 48 months were given another 50% thinning leaving the best single tree per plot. Thus all the trials used in this study had single tree plots at time of measurement of assessment traits.

Table 2.1 Site information for *E. grandis* progeny trials at J.D.M. Keet plantation and F_2 trial at KwaMbonambi plantation.

Site descriptors	**Plantation**	
	J.D.M. Keet	**KwaMbonambi**
Province	Limpopo	KwaZulu-Natal
Closest town	Politsi	KwaMbonambi
Latitude	23˚ 47' S	28˚ 38' S
Longitude	30˚ 07' E	32˚ 11' E
Altitude	750 m	30 m
Soil type	Hutton	Hutton
Effective Rooting Depth (ERD)	150 cm	150 cm
Mean Annual Precipitation (MAP)	1300 mm	1340 mm
Mean Annual Temperature (MAT)	20°C	21°C
Minimum annual temperature	6.3°C	10°C
Maximum annual temperature	29.8°C	30°C

Table 2.2 Site information for F_3 *E. grandis* trials at Silverfontein, Westfalia and Dukuduku plantations.

Site Descriptors	**Plantation**		
	Silverfontein	**Westfalia**	**Dukuduku**
Province	Limpopo	Limpopo	KwaZulu-Natal
Closest town	Politsi	Politsi	Mtubatuba
Latitude	23˚ 43' S	23˚ 44' S	28˚ 21' S
Longitude	30˚ 10' E	30˚ 06' E	32˚ 15' E
Altitude	750 m	950 m	70 m
Soil type	Hutton	Hutton	Fernwood
Effective Rooting Depth (ERD)	150 cm	150 cm	150 cm
Mean Annual Precipitation (MAP)	950 mm	950 mm	973 mm
Mean Annual Temperature (MAT)	20.6°C	20.6°C	22.5°C
Minimum annual temperature	6 °C	6 °C	7 °C
Maximum annual temperature	32 °C	32 °C	37 °C

Table 2.3 Trial designs for F_1 *E. grandis* trials (EA6206, EA6209, EA6210, EA6215, EA6218 and EA6221) at J.D.M. Keet plantation.

Trial Descriptors	**Trial**					
Trial number abbreviated	EA6206	EA6209	EA6210	EA6215	EA6218	EA6221
Design	RCB	RCB	RCB	RCB	RCB	RCB
Replications	9	9	9	9	9	9
Families	99	99	99	99	99	99
Number of plots	891	891	891	891	891	891
Plot size	2 x 2	2 x 2	2 x 2	2 x 2	2 x 2	2 x 2
Area (ha)	2.60	2.60	2.60	2.60	2.60	2.60
Espacement (m)	2.7 x 2.7	2.7 x 2.7	2.7 x 2.7	2.7 x 2.7	2.7 x 2.7	2.7 x 2.7
Compartment	21 & 22a	21 & 22	21 & 22	14	13a	4a
Date planted	12/1975	01/1978	01/1979	01/1981	01/1981	03/1983
Date clear felled	10/1981	09/1983	09/1984	09/1985	07/1987	08/1988
Assessed traits (age)	DBH, height (70 months), stem form (26 months)	DBH, height, stem form, volume, splitting, density (68 months)	DBH, height, stem form, volume, splitting, density, defects (68 months)	DBH, height, stem form, defects, splitting, spirality, crown (56 months)	DBH, height, stem form, defects; spirality (78 months)	DBH, height, stem form, defects; spirality, disease (65 months)

Table 2.4 Trial designs for the A-series F_2 *E. grandis* trials at J.D.M. Keet and KwaMbonambi plantations.

Trial Descriptors	**Trial**						
Trial number abbreviated	A1	A2.01	A2.02	A3	2A4	A5	A6
Plantation	J.D.M. Keet	J.D.M. Keet	KwaMbonambi	J.D.M. Keet	J.D.M. Keet	J.D.M. Keet	J.D.M. Keet
Design	Alpha lattice	Alpha lattice	Alpha lattice	Alpha lattice	Alpha lattice	Alpha lattice	Alpha lattice
Replications	9	9	9	9	9	9	9
Families	60 and 4 controls	61 and 3 controls	61 and 3 controls	69 and 3 controls	96 and 3 controls	96 and 3 controls	70 and 2 controls
Number of plots	576	576	576	648	891	891	648
Date selections were made in F_1 trials	1981	1983	1983	1984	1985	1986	1989
Plot size	2 x 2	2 x 2	2 x 2	2 x 2	2 x 2	2 x 2	2 x 2
Area (ha)	1.68	1.68	1.68	1.89	2.60	2.60	1.89
Espacement (m)	2.7 x 2.7	2.7 x 2.7	2.7 x 2.7	2.7 x 2.7	2.7 x 2.7	3.5 x 3.5	3.5 x 3.5
Date planted	03/1983	12/1983	04/1984	02/1985	10/1986	12/1988	03/1990
Date clear felled	03/1991	03/1991	07/1991	10/1991	10/1992	10/1994	10/1996
Assessed traits used in this study (age)	DBH, height, stem form, spirality, splitting, density, defects (91 months)	DBH, height, stem form, spirality, splitting, disease, hlb (81 months)	DBH, height, stem form, spirality, splitting, hlb, defects (81 months)	DBH, height, stem form, spirality, splitting, density, disease, hlb (76 months)	DBH, height, stem form, disease, splitting (72 months)	DBH, height, stem form, disease, splitting (67 months)	DBH, height, stem form, disease (62 months)

Table 2.5 Trial designs for the F_3 *E. grandis* trials at Dukuduku, Silverfontein and Westfalia plantations.

Trial Descriptors	**Trial**	
Trial number abbreviated	B4.01-B16.01	B4.02 -B16.02
Plantation	Dukuduku	Silverfontein Westfalia (B15.02 - B16.02)
Design	Alpha lattice	Alpha lattice
Replications	20	20
Families	50	50
Number of plots	1000	1000
Plot size	single tree	single tree
Area	0.90 ha	1.23 ha
Espacement	3 x 3 m	3.5 x 3.5 m
Date planted	05/1996 (B4 - B10) 06/1996 (B11 - B14) 08/1997 (B15 - B16)	05/1996 (B4 - B14) 06/1997 (B15 - B16)
Assessed traits used in this study (age)	DBH, height, stem, disease, defects (40 months; 51 months - B15 - B16)	DBH, height, stem, disease, defects (38 months; 25 months - B15 - B16)

The location within South Africa of the plantations of the *E. grandis* trials used in this study are depicted in Figure 2.4.

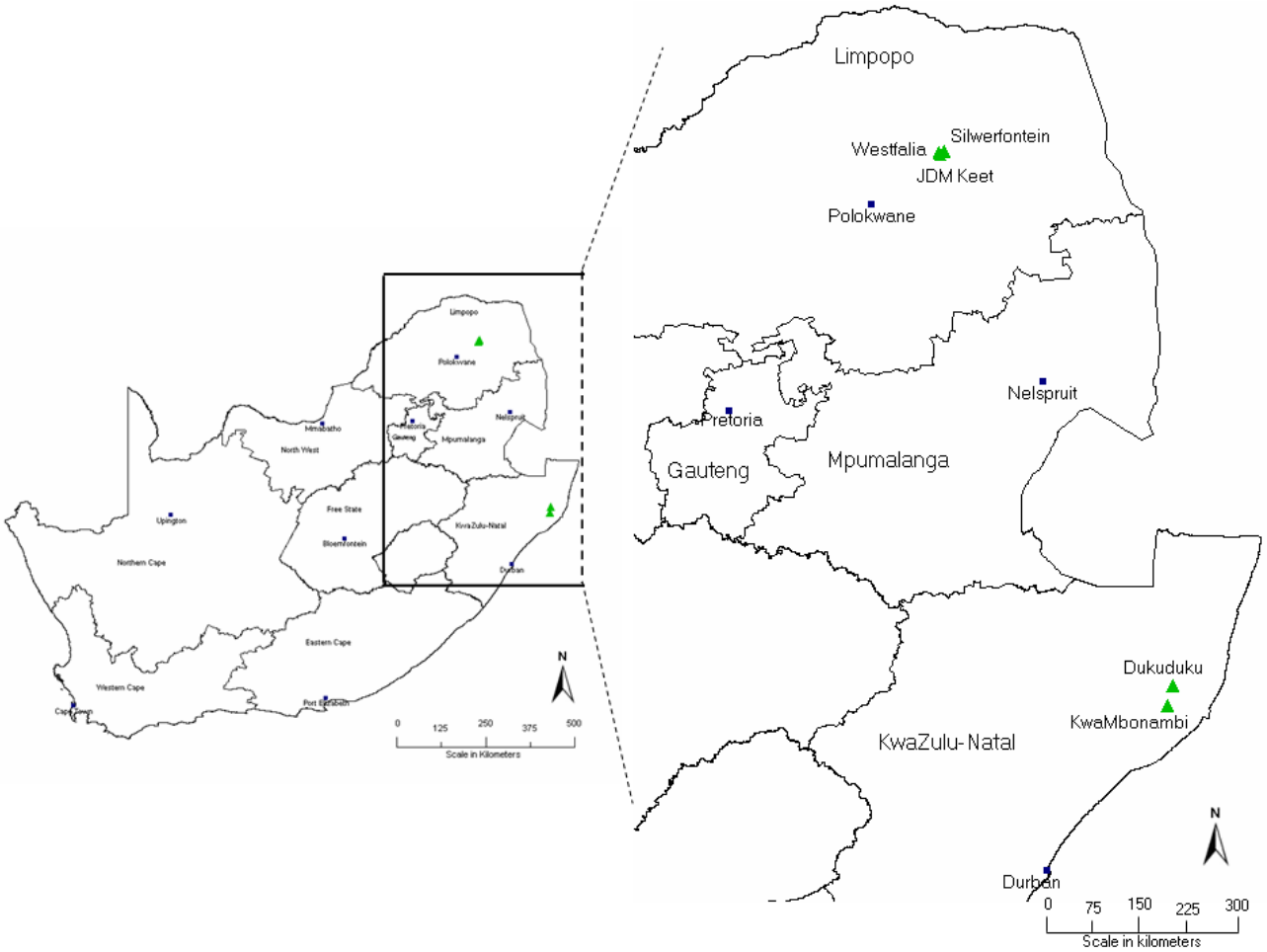

Figure 2.4 Locations of the *E. grandis* trials within South Africa.

2.3.1.2 Trial assessments and trait details

At or near the time of clear felling trials A1 - A4 were assessed for diameter at breast height (DBH), height, stem form, defects, log-end splitting, spirality and samples were taken from each tree for density determinations. Trial A4 was assessed for disease tolerance in addition to the above mentioned traits. Trial A5 was assessed for height, DBH, stem form, defects and disease tolerance three months prior to clear felling. At the time of clear felling in trial A5 a selection of 251 trees (based on the prior to felling data) were assessed for splitting and samples were taken for density assessments. Trial A6 was assessed for DBH, height, stem form and disease tolerance at 62 months and was clear felled 17 months later. Dates of clear felling are detailed in Table 2.4.

At the Dukuduku trials, height, diameter at breast height (DBH), stem form and disease tolerance were assessed at age 40 months (B-series trials B4.01 - B14.01) and 51 months (B-series trials B15.01 and B16.01). At the Silverfontein and the Westfalia trials, height, diameter at breast height (DBH), stem form and disease tolerance were assessed at 38 months (B-series trials B4.02 - B14.02) and 25 months (B-series trials B15.02 - B16.02) and density (pilodyn measurements) and splitting were assessed at six years (B-series trials B4.02 - B16.02).

Height was measured in metres using a height rod or a vertex hypsometer. Diameter at breast height (DBH) was measured over bark in centimetres at a height of 1.3 m above the ground using a diameter tape. Stem form was scored on a subjective eight point scale as shown in Table 2.6. The scale was used as a fixed scale and was not adjusted for sites. Disease tolerance was scored on a subjective five point scale, where zero represented no visual infestation and four represented chronic infestation. The log-end splitting counts were taken from the top end of the first 2.4 m log and the butt end of the second 2.4 m log for each tree and these counts were made 48 hours after felling. Spirality was assessed in degrees on the top end of the first 2.4 m log for each tree. Defects where they occurred were also noted.

Table 2.6 Description of scores used to assess stem form (straightness).

Score	Short description	Stem straightness defects associated with score
8	Straight	No defects
7	Nearly straight	1 – 2 minor defects
6	Very slightly crooked	3 – 4 minor defects
5	Slightly crooked	2 moderate defects or 2 moderate & 1 minor
4	Moderately crooked	1 moderate & 1 major or 2 moderate or 2 major & 2 minor
3	Crooked	2 major or 2 major & 2 moderate
2	Very crooked	Several major & moderate defects
1	Malformed	Major defects

The measured traits that were used in this study were diameter at breast height (DBH), height and stem form as these traits were present in all of the data sets and at similar measurement ages.

2.3.2 Broad background and history to the CSIR *Pinus patula* genetic resource

Breeding of *Pinus patula* in South Africa began in 1953 with the establishment of the first progeny trial at the Border plantation in the KwaZulu-Natal province consisting of 125 open-pollinated families (van der Merwe 1996).

The first tree breeding research centre was established at the old D.R. de Wet Forest Research Centre near Sabie in the Mpumalanga province in 1958. During the period from 1958 to 1995, nine first generation (P_0) seed orchards (see Figure 2.5) had been established (De Lange 1996). In 1991 all the breeding work previously completed by SAFRI was transferred to CSIR (Forestek division at the time). SAFCOL (South African Forestry Company) started its own breeding programme in 1993 with the *P. patula* material from the old SAFRI and Forestek programmes. *P. patula* research was conducted jointly by the CSIR and SAFCOL from 1996 to 1999 under the "Accelerated Tree Breeding Research partnership". The research focussed on the development of a *P. patula* breeding and production research strategy (van der Merwe 1999).

The basis of the breeding population was formed from a total of 1185 plus trees obtained from all the existing plantations. Plus trees are trees that have been selected based on their phenotypic appearance and have acceptable timber quality (Van Wyk 1993 cited in De Lange 1996). Open-pollinated seed was collected from the plus trees and planted into progeny trials for testing. Also included in these trials was seed obtained from selections of private companies and seed from overseas (van der Merwe 1999). A total of 801 families of the 1185 first generation selections from South Africa and 42 selections from Zimbabwe were included in progeny trials (see Figure 2.5). The Institute for Commercial Forestry Research (ICFR) made 146 selections on Merensky, Mondi and Sappi land which were tested in progeny trials. A total of 51 Mexican families were tested in progeny and provenance trials (van der Merwe 1996). There

were 41 progeny and 29 provenance trials established from 1953 to 1995 (van der Merwe 1996).

Second generation selections were made in the trials based on assessments made at ages between five and 13 years. A total of 671 second generation selections were made in the older provenance and progeny trials (see Figure 2.5).

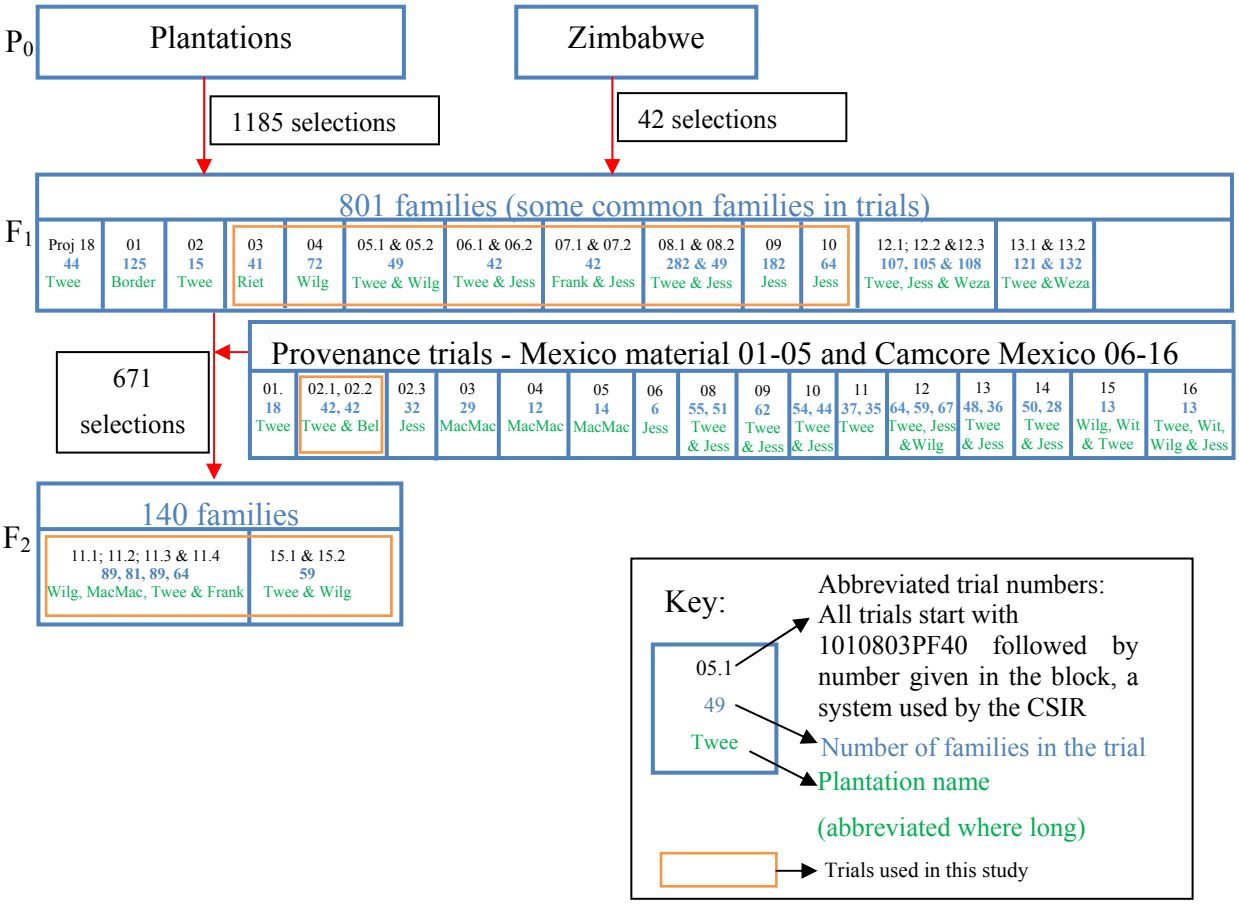

Figure 2.5 *P. patula* F_1 and F_2 breeding populations.

2.3.2.1 P. patula trials and genetic material used in this study

Plus tree selections were made from existing *P. patula* P_0 plantations based on visual selection of superior phenotypes and acceptable timber quality. Open-pollinated seed was collected from the plus trees and used to plant the F_1 provenance and progeny trials (as highlighted in the orange block in the F_1 generation shown in Figure 2.5). All the open-pollinated seed and seed for the controls were sown in nursery trays and planted

into the trials approximately 10 months later. *P. patula* F_1 trials used in this study included provenance trials 1010303PF4002.01 (PF4002.01) and 1010303PF4002.02 (PF4002.02) (Table 2.10) and progeny trials 1010803PF4003 - 1010803PF4010 (PF4003 – PF4010) (Table 2.9). The two provenance trials (PF4002.01 and PF4002.02) were planted at two sites (Table 2.7), consisting of 42 provenance treatments. Eight progeny trials were included in this study (Table 2.9). Four of these progeny trials were duplicated and planted at more than one site. A total of 695 first generation families were included in these progeny trials. The trials were planted between 1965 and 1983. Controls in the trials included commercial controls and seed orchard controls.

The provenance trials (PF4002.01 and PF4002.02) were planted in 1971 at Tweefontein and Belfast plantations in the Mpumalanga province. The progeny trials (PF4003, PF4004, PF4005.01 and PF4005.02, PF4006.01 and PF4006.02, PF4007.01 and PF4007.02, PF4008.01 and PF4008.02, PF4009 and PF4010) were planted at the Rietfontein (now known as Tweefontein), Wilgeboom, Mac-Mac (now also known as Tweefontein), Tweefontein, Jessievale and Frankfort plantations between December 1967 and March 1998. Details of the trials are shown in Tables 2.9 and 2.10.

The open-pollinated seed from selections from the F_1 trials were sown in Unigrow tubes in the nursery and used to establish the F_2 *P. patula* trials. *P. patula* F_2 trials included trials 1010803PF4011 and 1010803PF4015 (as shown in the F_2 block in Figure 2.5). For the details of the sites for the F_2 trials, 1010803PF4011 and 1010803PF4015 (PF4011 and PF4015), please refer to Tweefontein, Wilgeboom and Frankfort details given in Tables 2.7 and 2.8. A total of 89 families were included in trial PF4011 which was planted on four sites (Table 2.11). Two of the sites, contained only 81 and 64 families respectively. Three commercial controls were included at all the sites.

Trial PF4015 was duplicated at three sites and each site had the same 54 families and five controls (Table 2.11). Only two sites (Tweefontein and Wilgeboom) were used in this study due to a suspected error in the sequence in which the third trial planted at Jessievale plantation was measured.

During December 1989 three PF4011 trials were planted at Tweefontein plantation; Wilgeboom plantation and Mac-Mac (now known as Tweefontein) plantation. The fourth PF4011 trial at Frankfort was planted in January 1990. During February 1994 the three PF4015 trials were planted at Tweefontein, Wilgeboom and Jessievale plantations in the Mpumalanga province.

Table 2.7 Site information for *P. patula* F_1 provenance trials planted at Tweefontein and Belfast plantations.

Site descriptors	**Plantation**	
	Belfast	**Tweefontein**
Province	Mpumalanga	Mpumalanga
Closest town	Belfast	Between Sabie and Graskop
Latitude	25˚ 69' S	25˚ 03' S
Longitude	30˚ 04' E	30˚ 47' E
Compartment	A.11	A.32
Altitude	1888 m	1152 m
Mean Annual Precipitation (MAP)	not available	1298 mm
Mean Annual Temperature (MAT)	not available	17.6 °C

Table 2.8 Trial site information for *P. patula* F_1 progeny trials.

Site descriptors	**Plantation**			
	Wilgeboom	**Tweefontein**	**Jessievale**	**Frankfort**
Province	Mpumalanga	Mpumalanga	Mpumalanga	Mpumalanga
Closest town	Between Graskop and Bushbuckridge	Between Sabie and Pilgrim's Rest	Between Carolina and Lothair	Between Sabie and Hazyview
Latitude	24˚ 59' S	25˚ 03' S	26˚ 14' S	25˚ 02' S
Longitude	30˚ 48' E	30˚ 47' E	30˚ 31' E	30˚ 53' E
Trial Compartments	B36 (PF4004;PF4005.01)	C7 (PF4003)	E29 (PF4006.02; PF4007.01)	B10 (PF4007.02; PF4011.03)
	B32b (PF4011.01)	L38 (PF4005.02)	A118 (PF4008.02)	
	B26 (PF4015.01)	K16 (PF4006.01)	A10b (PF4009)	
		C57 (PF4008.01)	A7 (PF4010)	
		K36 (PF4011.02)		
		D16 (PF4015.03)		
Altitude	945 m	1152 m	1733 m	980 m
Mean Annual Precipitation (MAP)	1348 mm	1298 mm	908 mm	1467 mm
Mean Annual Temperature (MAT)	18.4°C	16.5°C	16.5°C	18.2°C

Table 2.9 Trial designs for *P. patula* F_1 trials (PF4003, PF4004, PF4005, PF4006, PF4007, PF4008, PF4009 and PF4010).

Trial Descriptors	**Trial**							
Trial number abbreviated	PF4003	PF4004	PF4005	PF4006	PF4007	PF4008	PF4009	PF4010
Plantation	Rietfontein	Wilgeboom	Wilgeboom (01) Tweefontein (02)	Tweefontein (01) Jessievale (02)	Jessievale (01) Frankfort (02)	Tweefontein (01) Jessievale (02)	Jessievale	Jessievale
Design	Random complete block	6 x 6 lattice (2 sets)	7 x 7 lattice	6 x 7 lattice (2 sets)	6 x 7 lattice	7 x 7 lattice (6 sets in Tweefontein)	7 x 7 lattice (4 sets)	8 x 8 lattice
Replications	10	4 per set	4	3 per set	6	8 per set	8 per set	9
Families	41	72 (only 67 in measured dataset)	49	42	42	285 (Tweefontein) 49 (Jessievale)	185	64
Number of plots	410	144	196	126	252	392	392	576
Plot size	4 x 4 square plots	1 x 10 row plots	1 x 10 row plots	1 x 10 row plots	1 x 6 row plots	1 x 6 row plots	1 x 6 row plots	1 x 6 row plots
Area (ha)	1.7	2.18	1.47	1.89	1.11	12.36 (Tweefontein) 1.98 (Jessievale)	6.8	2.52
Espacement (m)	2.7 x 2.7	2.7 x 2.7	2.7 x 2.7	2.7 x 2.7	2.7 x 2.7	2.7 x 2.7	2.7 x 2.7	2.7 x 2.7
Date planted	12/1967	01/1975	01/1975	03/1976	01/1979	03/1983	01/1985	03/1988
Date felled	1993	1992	1992				Not felled	Not felled
Assessed traits of data sets used in this study (age - months)	DBH, height, stem, crown, defects & density (108)	DBH, height, stem & defects (102)	DBH, height, stem, spirality & defects (100 – Wilgeboom; 166 – Tweefontein)	DBH, height, stem, branch angle & defects (96 - Jessievale; 65 - Tweefontein)	DBH, height, stem, crown & defects (104 – Jessievale; 97 – Frankfort)	DBH, height, stem, crown & defects (96)	DBH, height, stem & crown (96)	DBH, height, stem & crown (72)

Table 2.10 Trial designs for the *P. patula* provenance trials (PF4002.01 and PF4002.02) at Belfast and Tweefontein plantations.

Trial Descriptors	**Trial**
Trial number abbreviated	PF4002.01 PF4002.02
Plantation	Belfast Tweefontein
Design	6 x 7 lattice
Replications	3
Families	42 (Belfast) 29 (Tweefontein)
Number of plots	126
Plot size	4 x 4 trees
Area (ha)	1.5
Espacement (m)	2.7 x 2.7
Date planted	01/1971
Date felled	01/1993
Assessed traits of data sets used in this study (age - months)	DBH, height, stem, density & defects (156 months)

Table 2.11 Trial designs for *P. patula* F_2 trials (PF4011 and PF4015).

Trial Descriptors	**Trial**	
Trial number	1010803PF4011.01 - 0.4	1010803PF4015.01 - 0.2
Plantation	Wilgeboom Mac-Mac (Tweefontein) Tweefontein Frankfort	Tweefontein Wilgeboom
Design	Randomized complete block	Randomized complete block
Replications	20	20
Families	89 (Tweefontein & Wilgeboom) 81 (Mac-Mac) 64 (Frankfort)	59
Number of plots	1780 (Tweefontein & Wilgeboom) 1620 (Mac Mac) 1280 (Frankfort)	1180
Plot size	Single tree plots	Single tree plots
Area (ha)	1.30 (Tweefontein & Wilgeboom) 1.18 (Mac Mac) 0.93 (Frankfort)	0.86
Espacement (m)	2.7 x 2.7	2.7 x 2.7
Date planted	12/1989 (Tweefontein, Mac Mac & Wilgeboom 01/1990 (Frankfort)	02/1994
Assessed traits of data sets used in this study (age - months)	DBH, height, stem and crown (84 months)	DBH, height, stem and crown (96 months)

The location within South Africa of the plantations of the *P. patula* trials used in this study are depicted in Figure 2.6.

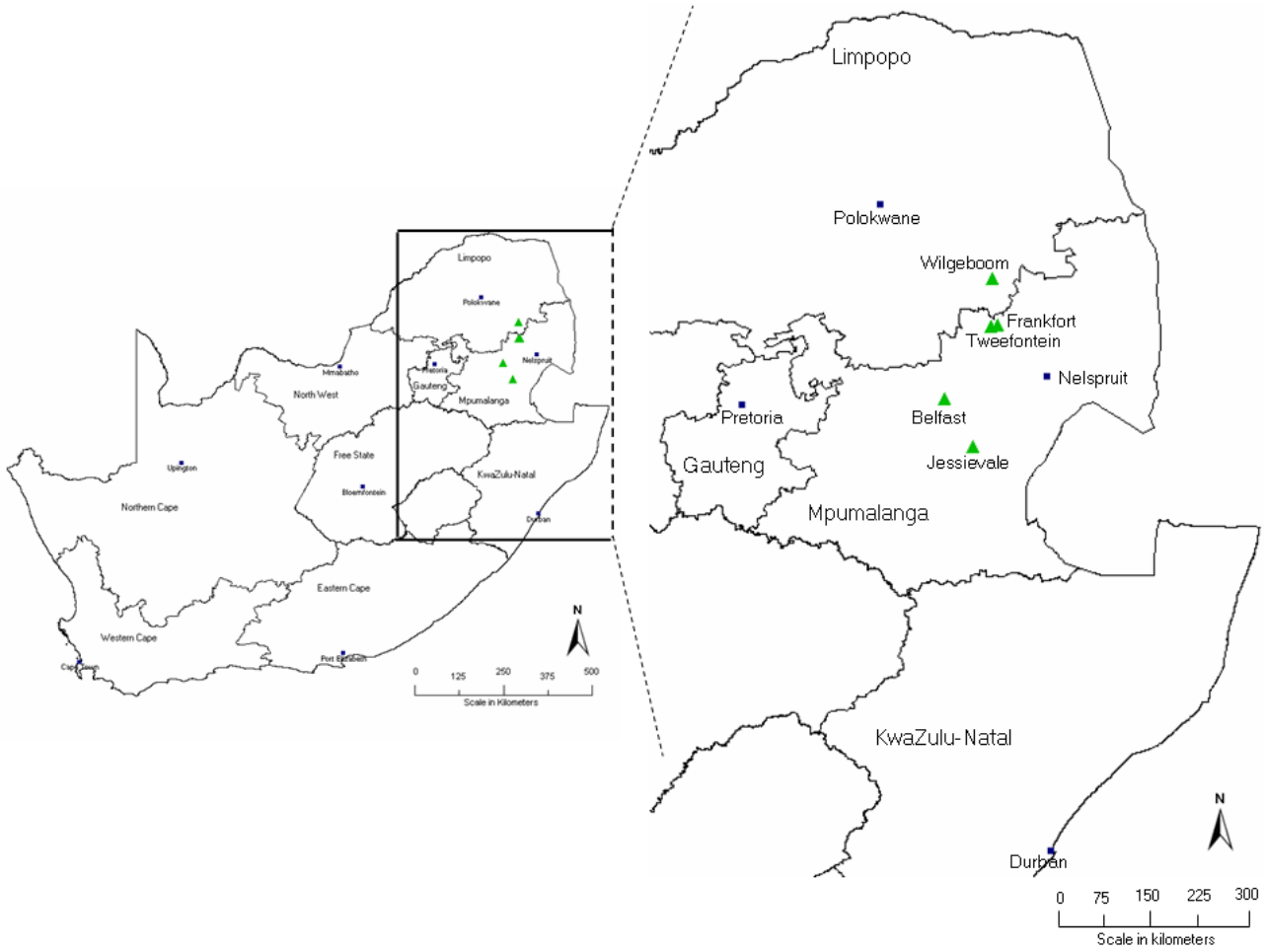

Figure 2.6 Locations of the *P. patula* trials within South Africa.

2.3.2.2 Trial assessments and trait details

The trial assessments for the F_1 *P. patula* trials used in this study for the predicted population data were of varying ages with date of planting from 1967 to 1988. Data of similar ages with traits of interest were not always available.

The data available for the two provenance trials (1010303PF4002) planted at Tweefontein and Belfast plantations were 13 to 14 year measurements of diameter at breast height (DBH), height, stem form, density (pilodyn measurements) and defects.

Trait assessments for the rest of the F_1 trials varied between 8 years and 13 years. Trial 1010803PF4003 at Rietfontein was assessed for DBH, height, stem form, crown form, density and defects. Trial 1010803PF4004 at Wilgeboom was assessed for DBH, height, stem form and defects. In trials 1010803PF4005 and 1010803PF4006, DBH, height, stem

form and defects were assessed and additional traits of density and spirality were also assessed respectively in these trials. DBH, height, stem form, crown form and defects were assessed in trials 1010803PF4007 and 1010803PF4008 at Jessievale, Frankfort and Tweefontein plantations. In trials 1010803PF4009 and 1010803PF4010 at Jessievale DBH, height, stem form and crown form were assessed.

DBH, height and stem form traits were measured as described in section 2.3.1.2 for the *E. grandis* trials. Crown form in the *P. patula* trials was assessed using a subjective six point scale which assessed the crown of the trees in terms of the distribution of branches and the lightness of the distribution. On the scale one denoted a tree with large branches closely distributed and six a tree with light branches far apart. The measured traits that were used in this study were DBH, height and stem form as in the *E. grandis* trials.

CHAPTER 3
METHODS

3.1 Introduction

The data from six F_1, seven F_2 and 26 F_3 *E. grandis* trials and 14 F_1 and six F_2 *P. patula* trials (discussed in Chapter 2) were analysed in order to assess which matrix inversion technique or adapted ridge regression technique used in Best Linear Unbiased Prediction (BLUP) selection calculations are best at dealing with situations where some degree of collinearity in the data may cause instability and affect some of the components of the models and additionally whether there are differences in results when using computer programmes with different numerical precision.

The methods used in this study are set out in Figure 3.1. The first step was an exploratory phase to assess what data were available for each trial and to choose data sets of similar ages where possible and the data were then edited. Genetic parameters were then estimated for the trials. A check was executed to assess whether there was a potential degree of collinearity in the data by using the phenotypic correlations between the three selection traits used for the study (DBH, height and stem form). Predicted breeding values were estimated in the F_1 and F_2 *E. grandis* trials and the F_1 *P. patula* trials using different matrix inversion techniques and an adapted ridge regression technique within BLUP. Realised breeding performance was estimated in the F_2 and F_3 *E. grandis* trials and the F_2 *P. patula* trials. Two versions of the same Best Linear Unbiased Prediction (BLUP) software package for unbalanced index selection in tree breeding called Matgen (Verryn and Geerthsen 2006) were developed by a software programmer and were used for the calculation of the breeding values (BLUP index values) in this study. These versions were developed from Matgen 5.1, a programme created by Verryn (1994). Matgen 5.1 was thoroughly tested by Verryn (1994) using simulated data and validated through comparisons with solutions from SAS IML (1988) and RESI 4 of Cotterill and Dean (1990), alternative programmes which were available at the time. These comparisons gave virtually (except for round-off error due to differences in the significant digits of values) identical solutions to Matgen 5.1 (Verryn

1994). In this current study, the predicted breeding values were correlated with the realised breeding performance in the estimation of the accuracy of prediction (see section 3.7 for the supporting theoretical background). Realised genetic gains were calculated for each technique used and for each economic weighting set. Here the relative performance of the progeny in the next generation using the backward BLUP values provided the best available measure for realised genetic gains. The BLUPs resulting from the different matrix inversion methods and ridge regression as well as the two numerical precision programmes, were compared using these measures of accuracy and realised genetic gains. The partial pivoting technique (see section 3.5.1) was used as the control where no collinearity mitigation technique was applied. Partial pivoting also served as a further indication of the potential presence of collinearity (a requirement for the data to be used in the study as mentioned in Chapter 2) in the data sets leading to instability in the calculations of the BLUP index values.

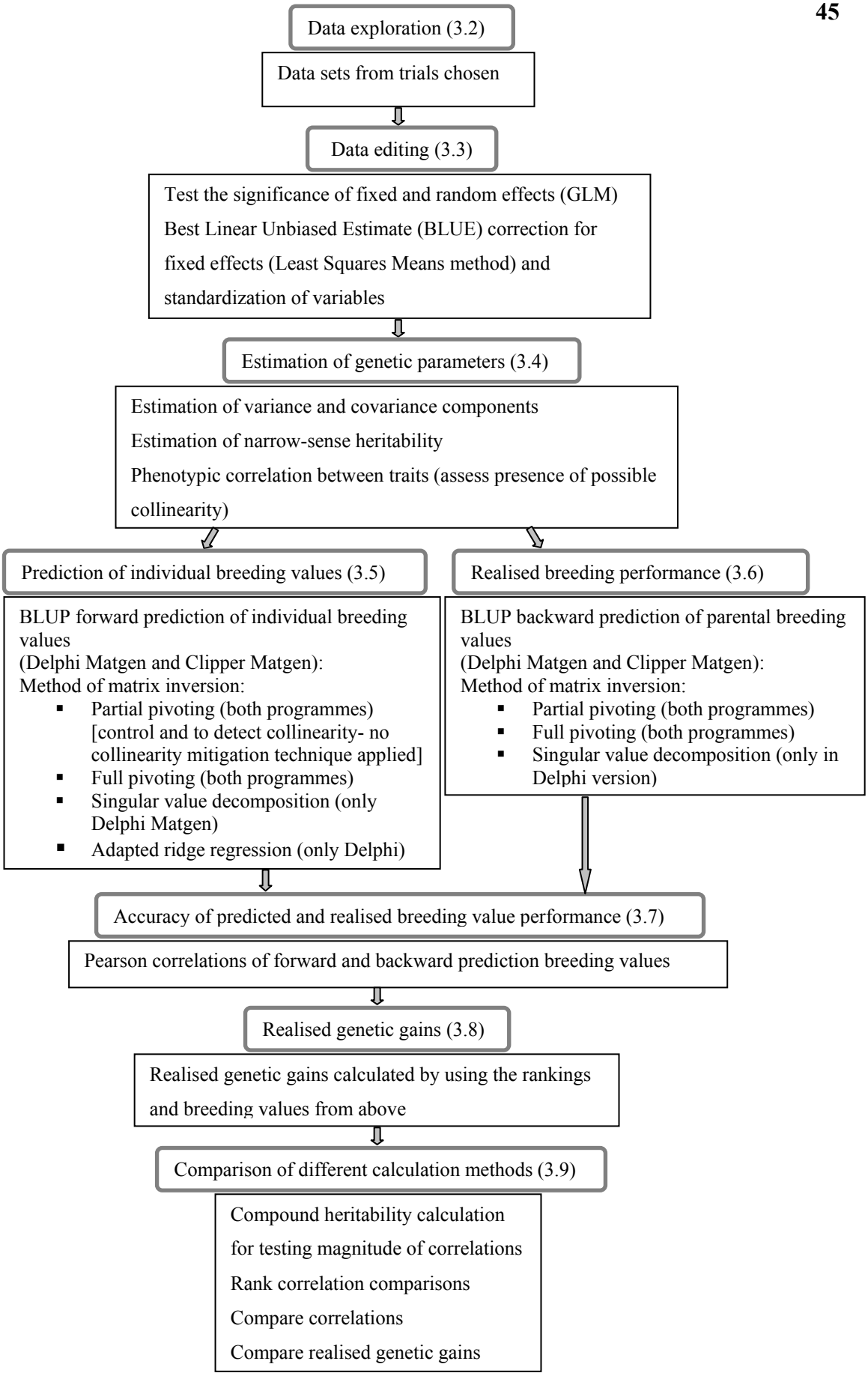

Figure 3.1 Methods used in this study. The relevant sections from this Chapter are indicated in brackets for each method.

3.2 Data exploration

The data exploration step involved an examination of all potential electronic data files of the *P. patula* and *E. grandis* breeding programmes of the CSIR to determine the suitability of the data for this study based on the criteria discussed in section 2.2. Data sets were chosen from similar aged assessments within each generation of trials where possible although the main criterion was that the same traits had to be available in each generation of trials.

Selection of trials was also based on available pedigree data detailing the selections made in each generation to plant the next generation of breeding trials.

The assessment traits that were used in this study were diameter at breast height (DBH), stem form and height as data was available for all these traits at suitable assessment ages for each generation of trials.

3.3 Data editing

The data analysis was carried out using SAS/STAT software, Version 9.1 of the SAS System for Windows. Copyright © 2002-2003 SAS Institute Inc. The data was edited before any other analysis was executed in SAS. Tests for normality, checks for outliers and missing data were run. Trees with missing observations and outliers (observations that that lay within 1.5 times the interquartile range (IQR) below the 25th percentile and those that lay 1.5 (IQR) above the 75th percentile i.e. trees with much smaller or larger DBH, height and stem form values) were deleted from the data sets. The data sets were unbalanced due to mortality in the trials.

The PROC GLM procedure in SAS was used to test for the significance of the fixed effects in the data sets. PROC GLM is a two-way mixed model ANOVA procedure that is suitable to use for unbalanced data. Both continuous variables and variables with discrete categories can be analysed using this procedure. In the data sets the families were considered as random effects and the replications to be fixed effects. The data sets were corrected for fixed replication effects using least squares means (LS-means). The

correction reduces the bias of selection from the good performing replications. Following the correction step in SAS the variables appear normally distributed as the normal method of Blom (1958) is used (SAS Institute Inc. 2004). The data sets were all also standardized in order to obtain more normal data, standardizing the variables to a given mean and standard deviation in SAS (method of Blom 1958 cited in SAS Institute Inc. 2004) resulting in the data having a mean of zero and a standard deviation of one. The advantage of having standardized data sets is that data sets from different ages can be compared because the data sets are independent of the ranges of actual values or units of measurements. Another advantage is that it simplifies the interpretation of the relative rankings of individuals in the BLUP index. For example where the trait score is zero it equals the trial average and a score of plus one equals one standard deviation more than the average.

The corrected and standardized values were obtained from the following equation in SAS:

$$y_{corrected} = y_{measured} - \bar{y}_{replication} \qquad (3.1)$$

where

$y_{measured}$ = standardized values for the trait

$\bar{y}_{replication}$ = Least Squares means for replication.

3.4 Estimation of genetic parameters

Narrow-sense heritability was estimated for all of the *E. grandis* and *P. patula* breeding trials. The narrow-sense heritability estimates served as verification for the breeding potential of the chosen traits and served as input for BLUP calculations.

The narrow-sense heritability is defined by the following equation as the ratio of the additive genetic variance to the phenotypic variance (Falconer 1989):

$$h^2 = \frac{\sigma_a^2}{\sigma_p^2} \qquad (3.2)$$

where

σ_a^2 = the additive genetic variance

σ_p^2 = the phenotypic variance.

The additive genetic variance is not measured directly and is estimated in different ways depending on whether the population consists of full-sibs or half-sibs. All of the trials used in this study consisted of open-pollinated half-sibs. The σ_a^2 was expressed in terms of the family variance.

The family component of variance (σ_f^2) was interpreted as the product of the coefficient of relationship and the additive genetic variance (Becker 1992; Falconer 1989):

$$\sigma_f^2 = R\sigma_a^2 \qquad (3.3)$$

The coefficient of relationship (R in equation 3.3) of 0.25 was used for the *P. patula* trials. This value of 0.25 has historically been used in calculating heritabilities in the *P. patula* trials that form part of the CSIR breeding programme and was kept as such in this study. It is believed that there was little or no inbreeding or selfing in these trials. This assumption has since been questioned (Kanzler 2002; Stanger 2003; Vermaak 2007). In the open-pollinated *E. grandis* trials a degree of selfing (or related crossing) is expected in the trials. In a study using comparisons between heritabilities of open- and control-pollinated *E. grandis* in the same trials, it was suggested that there may be as much as twenty percent natural selfing in open-pollinated populations (Verryn 1993). Verryn (1993) therefore recommended that the coefficient of relationship should be increased from 0.25 to 0.30 for half-sibs in selection and heritability procedures of open-pollinated populations of *E. grandis*. Similar results for selfing in *E. grandis* were found by Griffin *et al.* (1987); Griffin & Cotterill (1988); Hodgson (1976a) and

Hodgson (1976b). Based on the above mentioned recommendations, a coefficient of 0.3 was used for the *E. grandis* trials in this study.

The Mixed Model Least-Squares and Maximum Likelihood programme (LSMLMW & MIXMDL PC-2 Version) developed by Harvey (1990a) was used to estimate the genetic variance components needed for BLUP index calculations and to calculate the narrow-sense heritabilities for the assessed traits in each trial.

Two model options of the LSMLMW programme of Harvey (1990a and 1990b) are most frequently used in tree breeding trials, namely model two and model six. Model two of the programme may be used for trials which have single tree plots and for which there are no family-replication interaction effects (Harvey 1990a, Harvey 1990b). In this study model two was used in the *E. grandis* trials and the *P. patula* F_2 trials- which were single tree plots trials- and model six for the F_1 *P. patula* trials which had multiple tree plots.

The models are defined by the following equations (Harvey 1990a):

Model two:

$$y_{ijk} = \mu + E_i + f_i + e_{ijk} \qquad (3.4)$$

Model six:

$$y_{ijk} = \mu + E_i + f_i + (Ef)_{ij} + e_{ijk} \qquad (3.5)$$

where

μ = a population mean

E_i = fixed effect

f_i = random effect

e_{ijk} = random error

$(Ef)_{ij}$ = interaction between the fixed and random effect

y_{ijk} = the ijkth observation.

The genetic covariance components were calculated from the among family covariance as determined by the LSMLMW programme of Harvey (1990a).

Cov(genetic) = 1/R x Cov(among)

where

Cov(genetic)	=	genetic covariance
R	=	coefficient of relationship
Cov(among)	=	among family covariance from Harvey output.

3.5 Prediction of individual breeding values

Individual breeding values (forward prediction) were predicted in the F_1 population data of the *P. patula* and *E. grandis* trials as well as the F_2 population data of the *E. grandis* trials using BLUP. A Best Linear Unbiased Prediction (BLUP) software package for unbalanced index selection in tree breeding called Matgen (Verryn & Geerthsen 2006) was chosen for the purpose of this study. Although other software programmes exist for the calculation of BLUP values in forestry data such as ASReml (Gilmour *et al.* 2009) and TREEPLAN (Kerr *et al.* 2001) it was decided to use Matgen for this study as adaptations to the programme could easily be made to allow for various options of matrix inversion and to test for the effect of different numerical precision. As the generalised least squares means correction for fixed effects is used and thus effectively the BLUE (Best Linear Unbiased Estimates) values are input into Matgen, the solution for the predicted breeding values is therefore the BLUP solution (White & Hodge 1989; Verryn 1997).

The following equation (shown in matrix format) from White and Hodge (1989) is used in calculating the breeding values in the Matgen programme:

$$\hat{g} = \mathbf{a}\mathbf{C}'\mathbf{V}^{-1}(\mathbf{y} - \alpha) \qquad (3.6)$$

where

$\hat{g}$ = the vector of the predicted breeding value for the individual within a particular family (forward prediction denoted as $\hat{g}_{fwd}$ in this study) or the parent (backward prediction $\hat{g}_{bwd}$ in this study)

a = the vector (qx1) of q economic weights

C = the mxq matrix of genotypic variances and covariances between observations on a single candidate and its siblings (forward prediction) or on a parent (backward prediction), of each selection trait

V = the mxm matrix of phenotypic variances and covariances among observations, for a single candidate and of the means of its siblings at each trial site (forward prediction) or for the parent (backward prediction) at each trial site, of each selection trait

y = the mx1 vector of phenotypic observations relating to a candidate for selection, which may include observations such as individual measurements and family means at each trial site (forward prediction) or family means at each trial site (backward prediction), of the selection traits

α = E(y) is the mx1 matrix of expected values of observed data relating to each candidate (forward prediction) or parent (backward prediction).

The predicted breeding value thus combines information from all traits of interest into a single index value and all traits under consideration have economic weights and genetic information attached to them. The choice of suitable economic weights is important as it affects the efficiency of the index (Falconer 1989; Zobel & Talbert 1984).

In order to test the effect of differences in numerical precision, two versions of Matgen were used. One version of Matgen (Matgen5n) was written in DOS-based Clipper (Computer Associates 1993) and has 16-bit computational numerical precision. This Clipper version was a modified version of the Matgen 5.1 (Verryn 1994) programme. The other version of Matgen (Matgen 7.2) was written in Borland Delphi and has 32-bit

computational numerical precision. The analytical and mathematical procedures in both the Clipper and the Delphi programmes were identical, the only key difference being the operational level of numerical precision.

In this study different techniques for the mitigation of collinearity were included in Matgen (different matrix handling techniques for the inversion of the V matrix) in the calculations of the BLUP values (predicted ĝ values). The matrix inversion techniques used in the calculations of the BLUP values were Gaussian elimination (Gauss-Jordan method Press *et al.* 1992) with partial pivoting (referred to as Matgen 56 subroutine, Verryn 1994; and served as control), Gaussian elimination (Gauss-Jordan method) with full pivoting (Press *et al.* 1992) and singular value decomposition (SVD) (Press *et al*. 1992). An adaptation of ridge regression (Hoerl & Kennard 1970a) method was also included in the Delphi Matgen programme. The SVD method was also only used in the Delphi Matgen programme.

3.5.1 Gaussian elimination (Gauss-Jordan method)

Gauss-Jordan is an efficient method for inverting a matrix and is also as stable as any of the other direct methods (Press *et al*. 1992). The sequence of operations that are performed in Gauss-Jordan elimination is very closely related to those in other routines such as singular value decomposition (Press *et al*. 1992).

Gauss-Jordan elimination uses one or more operations such as interchanging of any two rows, interchanging of any two columns and replacing of a row by a linear combination of itself and any other row, to reduce a matrix to the identity matrix (matrix with diagonal elements all equal to one and all other elements equal to zero) (Press *et al*. 1992). In Gauss-Jordan elimination the elements above the diagonal are made zero at the same time that zeros are created below the diagonal and the diagonal of ones is made at this time too (Gerald & Wheatley 2004).

The difference between the two Gauss-Jordan methods used in Matgen was only the difference in pivoting. In partial pivoting an interchanging of rows is performed and in

full pivoting an interchanging of rows and columns is performed (Press *et al*. 1992) in the solution of the matrix inversion.

3.5.2 Singular Value Decomposition (SVD)

Singular value decomposition (SVD) is a powerful set of techniques used to deal with equations and matrices sets which are either singular or numerically very close to singular (Press *et al*. 1992). SVD often diagnoses problems in matrices where Gaussian elimination and Lower Upper Decomposition (another commonly used method) fail to give satisfactory results and in some cases SVD may even provide a useful numerical answer (Press *et al*. 1992). SVD methods are based on a linear algebra theorem which states that any m x n matrix A (where the number of rows m are greater than or equal to the n number of columns) can be written as the product of a m x n column-orthogonal matrix U, an n x n diagonal matrix W (having positive or zero elements) and the transpose of an n x n orthogonal matrix V as follows: $A = U.W.V^T$. U and V matrices are orthogonal in that their columns are orthonormal so that $U^T.U = V^T.V = 1$. (Press *et al*. 1992)

If matrix A is an n x n square matrix for example, then U, V and W are all square matrices of the same size. The inverses of U and V are equal to their transposes and for the diagonal matrix W, its inverse is the diagonal matrix whose elements are the reciprocals of the element w_j. The inverse of A is then $A^{-1} = V.[\text{diag}(1/w_j)].U^T$. Problems can occur in this construction when one of the w_j's is zero or if it is numerically so small that its value is dominated by round off error and unknowable. The matrix becomes more singular if more than one of the w_j's has this problem. (Press *et al*. 1992)

The SVD method makes use of a condition number of the matrix to indicate the singularity of the matrix. It is defined as the ratio of the largest of the diagonal matrix elements (w_j's) to the smallest of the elements (w_j's) (Press *et al*. 1992). A matrix is singular if its condition number is infinity and it is ill-conditioned or unstable if its condition number is too large i.e. if its reciprocal approaches the machine's floating

point precision (Press *et al*. 1992). The w_j elements that are responsible for the unacceptably large condition numbers will give rise to highly inflated elements in A^{-1}. The SVD method identifies the problem matrices in this way and the procedure replaces the small w_j elements that result in the large values, with zero. It can be shown that in the case of the familiar set of simultaneous equations A.x = b, the SVD procedure does not exactly solve the vector x, but finds the x that minimizes the residual |A.x-b| (Press *et al*. 1992). The values are zeroed at a threshold value. In Matgen this value has been chosen to be $1x10^{-6}$ which is a typical but not universal value and can be changed at the user's discretion. In this study the values of $1x10^{-1}$ and $1x10^{-2}$ were also used.

3.5.3 Adaptation of Ridge Regression

The adaptation of ridge regression (Hoerl & Kennard 1970a) that was used in this study, involved the addition of a positive constant k to the diagonal elements of the Identity matrix as follows (Verryn 1994; Verryn *et al*. 1995):

$$\hat{\beta}_p = \left[\mathbf{C}'\mathbf{V}^{-1} + k\mathbf{I}\left(\mathbf{C}'\mathbf{V}^{-1}\right)\right]\mathbf{a} \qquad (3.7)$$

where

$\hat{\beta}_p$ = ridge prediction coefficients

I = the identity matrix

k = constant ($k \geq 0$)

a = the vector of (1xq) of q economic weights.

Please refer to equation 3.6 for the definitions of **C** and **V**.

The resulting ridge coefficient is a biased estimate which may have decreased variances, but these can decrease more rapidly than the bias increases and thus the choice for data with a large amount of collinearity is between small bias, k, or large variance (Leath & Carroll 1985). A different k value was applied to each treatment at each site for the

ridge runs in this study based on the ridge trace method and graphical observation and also based on the behaviour of the condition number in the SVD inversion run.

3.5.4 Models for forward prediction

The breeding trials that were to serve as the predicted population data were run with forward prediction. In forward prediction the individual breeding values for the treatments (in this study the individual trees in a family of *E. grandis* or *P. patula*) are calculated and individuals are selected based on their predicted breeding values using their phenotype and their relative's (siblings') phenotype. The performance of the progeny is assumed not available in this model.

The forward prediction used in Matgen is expressed in terms of the following linear model:

Forward selection:

$$y_{ijkl} = \mu_i + E_{ij} + f_{ik} + e_{ijkl} \qquad (3.8)$$

where

y_{ijkl}	=	individual observation of a trait i of an individual
μ_i	=	a population mean for the trait i
E_{ij}	=	fixed effect for the i^{th} trait in test environment j
f_{ik}	=	random effect for trait i of family k
e_{ijkl}	=	random error for trait i of the l^{th} tree of family k in test j.

Multiple-site and multiple-trait analyses were carried out for both the *E. grandis* and the *P. patula* data for the purposes of this study. The *E. grandis* data from the F_1 trials and the data from the F_2 trials were each combined and run with forward prediction. The *P. patula* data from the F_1 trials were also combined and run with forward prediction.

To test the BLUP performance over generations under different economic weight scenarios and to provide a further means to possibly create examples of instability in the BLUP calculations for testing the mitigation methods, a set of 10 different chosen

combinations of economic weightings (see Table 3.1 below) were used and run for each of the different inversion methods and adapted ridge regression described above for the forward and backward prediction runs in Matgen.

Multiple-site with single trait scenarios were also run for comparison purposes.

Table 3.1 Economic weightings applied to the selection traits in the study.

Set No.	Economic weightings		
	DBH	Height	Stem form
1	0.2	0.4	0.4
2	0.4	0.4	0.2
3	0.15	0.6	0.25
4	0.1	0.7	0.2
5	0.7	0.2	0.1
6	0.2	0.1	0.7
7	0.3	0.2	0.5
8	0.5	0.3	0.2
9	0.8	0.1	0.1
10	0.1	0.1	0.8

3.5.5 Identifying instability in Matgen

Instability in breeding may be detected when one or more of the ß-coefficients of the solution for the Best Linear Unbiased Prediction are disproportionately large or small or the wrong sign (positive or negative), in relation to what is the logical expectation from a breeding point of view (Verryn 1994; Verryn *et al.* 1995; Verryn & Roux 1998). These 'wrong sign' coefficients would, for instance, result in the negative of an observation/family mean being included in the prediction of a breeding value where the value should intuitively be positively weighted. Matgen indicates possible instability cases in terms of "wrong sign" coefficients. The Matgen software output marks the unstable individuals (in forward selection models) with asterisks and also indicates the total number of unstable cases for the particular scenario that was run.

3.6 Realised breeding performance

The Matgen programme that was used for the forward prediction of breeding values was also used to estimate the realised breeding performances by means of backwards prediction. As described for the forward prediction, different versions of Matgen were used to monitor the effect of different numerical precision and different matrix inversion options and the same set of economic weighting options were used (Table 3.1).

3.6.1 Models for backward prediction

The F_2 (*P. patula* and *E. grandis*) and F_3 (*E. grandis*) trials that were to serve as the realised population were run with backward prediction. In backward prediction the breeding values for the parents are calculated using data from progeny of the selection or parent (Falconer 1989).

The backward prediction used in Matgen is expressed in terms of the following linear model:

Backward selection:

$$\bar{y}_{ijk.} = \mu_i + E_{ij} + f_{ik} + \sum \frac{e_{ijkl}}{n_{ijk}} \qquad (3.9)$$

Where

$\bar{y}_{ijk.}$ = the k^{th} family mean for trait i in test j

μ_i = a population mean for the trait i

E_{ij} = fixed effect for the i^{th} trait in test environment j

f_{ik} = random effect for trait i of family k

e_{ijkl} = random error for trait i of the l^{th} tree of family k in test j

n_{ijk} = the number of trees in family k in test j for trait i

The data from the *E. grandis* F_2 were run with backward prediction to serve as the 'realised' ranking for the F_1 selections. The *E. grandis* data from F_3 trials at each of the different site locations (Silverfontein and Dukuduku) were combined and were run with

backward prediction to serve as a 'realised' ranking of the F_2 *E. grandis* selections. The *P. patula* data from the F_2 trials were combined and run with backward prediction to serve as the 'realised' ranking of the F_1 selections. The F_2 trials represent progeny of selections of the F_1 trials and the F_3 trials represent progeny of selections of the F_2 trials. The study centred on the selections that gave rise to part of the next generation and their families. This may result in a measure of selection bias and may result in lower than expected intergenerational correlations.

3.7 Accuracy of predicted and realised breeding performance

The quality of predicted breeding values will depend on the amount and type of information used. A measure of this quality is the correlation between the true and predicted breeding values (Mrode 1996; Falconer & Mackay 1996, Cameron 1997 cited in Postma 2006). Postma (2006) refers to the correlation as the accuracy r of the predicted breeding values where $r = \{\sigma^2(\hat{a}) / \sigma^2(a)\}^{1/2}$. In this equation a is the true breeding value, â is the predicted breeding value and the variance of the true breeding value is equal to the additive genetic variance. The squared correlation between predicted and true breeding value is the reliability and is equal to the proportion of the additive genetic variance that is accounted for by the predicted breeding values (Postma 2006). This measure of precision is also used and defined by White and Hodge (1989) and given as $\text{Corr}(g,\hat{g}) = \{\text{Var}(\hat{g}) / \text{Var}(g)\}^{1/2}$ where $\hat{g}$ is the predicted values and g the true values. In this study the predicted breeding value was given as $\hat{g}_{fwd}$ and estimated from forward prediction (as described in section 3.5). The backward predicted breeding performance ($\hat{g}_{bwd}$) of the parents in the next generation of breeding provided the best available measure for the realised or true breeding value part of the Postma (2006) or White and Hodge (1989) accuracy estimation defined above. A similar principle to that of accuracy or precision as used by Postma (2006) and White and Hodge (1989) was thus used in this study. The accuracy was determined by the correlations between the forward predicted breeding values ($\hat{g}_{fwd}$) of one generation and the realised backward breeding performances ($\hat{g}_{bwd}$) of the next generation.

Pearson correlation coefficients between the BLUP values from the backward prediction runs ($\hat{g}_{bwd}$) and the BLUP values from the forward prediction runs ($\hat{g}_{fwd}$) for each set of

economic weightings and the particular matrix inversion technique and ridge regression technique were calculated in SAS using PROC CORR and the values were compared.

The data sets from the various Matgen runs of the F_1 trials were merged (in SAS using the merge statement) with a pedigree data set which contained all the treatments that were originally selected from the F_1 trials to be incorporated into the F_2 trials. These data sets were then used for the calculations of the correlation coefficients. The same procedure was followed with the forward prediction runs of the F_2 *E. grandis* trials which were merged with a pedigree data set which contained all the treatments that were originally selected from the F_2 trials to be incorporated into the F_3 trials. After the merging procedure treatments that were not part of the pedigree data set were removed thereby creating data sets that only contained the selected treatments and excluded all other treatments for using in the correlation calculations.

In the forward prediction runs of the *E. grandis* F_2 population data it was found that there were a number of large breeding values ($\hat{g}_{fwd}$ values). The $\hat{g}_{fwd}$ values that were greater than 2 and those that were less than -2 were removed in an exploratory run from the data set to be used for the calculation of the accuracy (correlation coefficients). Both resulting accuracy estimates (those including the large $\hat{g}_{fwd}$ values and those excluding the large $\hat{g}_{fwd}$ values are included in the results section for *E. grandis* in Chapter 4).

3.8 Realised genetic gains

Realised genetic gains in this study are expressed in terms of standard deviation units and were calculated from backward selection breeding values for each economic weighting set and each of the matrix inversion methods (Delphi and Clipper Matgen) and ridge regression runs. The data from the forward prediction runs for each scenario were sorted by rank and a top and bottom percentage of rankers were chosen. The hypothetical realised gain was obtained for the above mentioned forward selected trees by using the mean of the corresponding backwards selection breeding values ($\hat{g}_{bwd}$) (performance of the open-pollinated progeny in the F_2 (*E. grandis* and *P. patula*) or F_3 (*E. grandis*) trials). Others such as Hodge and White (1992), Ruotsalainen and

Lindgren (1998) and Silva *et al.* (2000) have used this method of calculating genetic gains as the mean of the breeding values. Realised genetic gain was calculated as the average of the breeding values for the top percentage and the bottom percentage of families. The percentages to use were based on the size of the data set (number of common families over generations) and the top five and bottom five percent was used for the *E. grandis* (F_1F_2 *E. grandis*: 451 common families; F_2F_3 *E. grandis*: 318 common families) and 10 percent was used in the case of the *P. patula* where there were fewer common families (F_1F_2 *P. patula*: 71 common families). The variance of the realised genetic gains among (mitigation) techniques within scenarios was also calculated.

3.9 Comparison of different calculation methods

The breeding value prediction results using the different matrix inversion methods and ridge regression technique were compared based on the ranks, number of unstable cases detected and the accuracy of predictions (White & Hodge 1989; Mrode 1996; Falconer & Mackay 1996; Postma 2006) (correlations of the predicted breeding values and realised breeding performance).

In order to evaluate the accuracy of prediction scores, a benchmark value was required. As a compound heritability was calculated for the balanced case, and the data is unbalanced, it may possibly be biased upwards. This benchmark value was calculated in the following manner:

The correlation between parent and offspring, in the absence of selection is equal to $(1/2)h^2$ from Falconer (1989). Hence, excluding the bias due to historic selection, the correlation between the forward and backward prediction breeding values should be of the order of one half of the heritability of the compound weighted trait ($1/2\,h^2_{c_i}$). The heritability of the compound weighted trait is defined as the following for this study:

$$h^2_{c_i} = \sum_{it} a_{it} \sum_{s} (h^2_{ts} / n) \qquad (3.10)$$

where

h^2_{ci} = heritability of the compound weighted trait for iteration i

a_{it} = the economic weight of trait t for iteration i, trait t =1 to 3

h^2_{ts} = heritability of trait t at site s for iteration i. The relevant heritabilities of a particular trait and site are the same for the iterations with that trait and site.

n = number of sites.

Chapter 4
RESULTS: *EUCALYPTUS GRANDIS* TRIALS

4.1 Introduction

There were six F_1, seven F_2 and 26 F_3 *E. grandis* trials from the CSIR eucalypt breeding programme available with suitably aged data and traits to investigate the remediation of potential instability in Best Linear Unbiased Prediction (BLUP) in tree breeding population data. Genetic parameters were estimated for these trials and the predicted breeding values estimated using different matrix inversion techniques and adapted ridge regression within BLUP. The realised breeding performance was also estimated using the same techniques as for the predicted breeding values within BLUP. The accuracy of the predicted breeding values and the realised breeding performance (correlations) and the different matrix inversion techniques were compared. The results from these *E. grandis* trials are presented in this chapter.

4.2 Data Editing

The data sets from all the trials were edited prior to any other analysis. Tests for normality of data and significance of effects were carried out for the three traits to be used in the BLUP index. The missing trees and any outliers (as described under 3.3 in the Methods chapter, Chapter 3) were deleted from the data sets before the main analysis was carried out.

4.2.1 Tests for Normality

All trials were analysed to assess whether the residuals were normally distributed prior to removal of missing data and outliers and correction and standardisation of variables. The tests of normality that were used included the Shapiro-Wilk statistic, skewness, kurtosis and normal probability plots of residuals.

The null hypothesis of the Shapiro-Wilk test is that the residuals are normally distributed. The Shapiro-Wilk value (W) is greater than zero and less than or equal to one. At a 5% level of significance, values of p that are greater than 0.05 will lead to the acceptance of the null hypothesis and indicate values are normally distributed. The Shapiro-Wilk test values are presented in Table 4.1 and Table 4.2. In the F_1 *E. grandis* trials, for the DBH variable, the Shapiro-Wilk test indicated that only trials 1010802EA6209 and 1010802EA6210 were normally distributed. The height variable only had trial 1010802EA6209 with normally distributed values. The Shapiro-Wilk test indicated that none of the F_1 trials had normally distributed values for the stem form variable. In the F_2 *E. grandis* trials, for the DBH variable, the Shapiro-Wilk test indicated that trials 1010802EA62A1, 1010802EA62A3 and 1010802EA62A4 values were normally distributed. In all the F_2 trials, for the height and stem form variables, the Shapiro-Wilk test indicated a departure from normality. In the F_3 *E. grandis* trials at both the Dukuduku and Silverfontein plantations, the Shapiro-Wilk test indicated a departure from normality for all the traits in all the trials.

Skewness and kurtosis are measures of the shape of the variable distributions. Distributions which are completely normal will have zero values for both skewness and kurtosis. Skewness measures the tendency of the distribution of data values to be more spread out towards one extreme with positive skewness values indicating values greater than the mean being more spread out and negative values indicating values less than the mean are more spread out. The skewness and kurtosis values for the *E. grandis* trials are presented in Table 4.1 and Table 4.2. Most trials had negative skewness values. Kurtosis gives a measure of the heaviness of the tails of the distributions. In some of the trials large positive kurtosis values indicated a leptokurtic distribution of data. Only a few trials had small negative kurtosis values indicating a platykurtic distribution of data.

The last measure of normality considered was the normal probability plots of the residuals. The normal probability plot plots the empirical quantiles against the quantiles of the standard normal distribution. When the data are normally distributed the probability plot forms an approximately straight line (Ott 1988). The normal probability plots are shown in Figure 4.1, Figure 4.2, Figure 4.3 and Figure 4.4.

All the trials showed some deviations from normality. After the removal of outliers and missing values from the data, the normality of the distributions was improved and smaller deviations were observed (skewness and kurtosis values closer to zero). All data were corrected for fixed effects and also standardized which normalises the variables (as mentioned in Chapter 3 section 3.3). Where possible methods were used in further analysis that are more suited to data which is unbalanced and not completely normally distributed (such as the generalised least squares methods (GLM) and restricted maximum likelihood (REML) methods). BLUP can handle data which is not completely normally distributed and deviations from normality do not decrease the accuracy of the estimated breeding values derived from BLUP (Goddard 1992).

Table 4.1 Normality of residuals test statistics for the F_1 and F_2 *E. grandis* trials.

Trial	**Trait**	**Normality of distribution test statistics**		
		Shapiro-Wilk Pr < W	**Skewness**	**Kurtosis**
1010802EA6206	DBH	<0.0001	-0.5196	1.7739
	Height	<0.0001	-0.5463	1.4804
	Stem form	<0.0001	0.1460	0.9193
1010802EA6209	DBH	0.1837	0.1835	-0.0760
	Height	0.0954	-0.2136	-0.1270
	Stem form	0.0005	0.0384	-0.6879
1010802EA6210	DBH	0.0692	0.2249	-0.0067
	Height	0.0013	-0.1230	0.9242
	Stem form	0.0007	-0.1333	-0.6173
1010802EA6215	DBH	0.0271	-0.0533	0.7995
	Height	0.0036	-0.2154	0.9408
	Stem form	<0.0001	-0.7393	2.6554
1010802EA6218	DBH	0.0011	-0.1378	0.2377
	Height	<0.0001	-0.9584	3.8409
	Stem form	<0.0001	-0.9858	2.1349
1010802EA6221	DBH	<0.0001	0.0547	1.1764
	Height	<0.0001	-0.3174	1.8359
	Stem form	<0.0001	-0.3917	0.1833

Trial	Trait	Normality of distribution test statistics		
		Shapiro-Wilk Pr < W	Skewness	Kurtosis
1010802EA62A1	DBH	0.5960	0.1430	0.0641
	Height	0.0010	-0.3143	0.5255
	Stem form	<0.0001	0.1206	0.4389
1010802EA62A2.01	DBH	0.0016	0.0014	0.8402
J.D.M. Keet	Height	<0.0001	-0.4514	1.4297
	Stem form	<0.0001	-1.2316	3.6915
1010802EA62A2.02	DBH	0.0003	-0.3716	0.2850
KwaMbonambi	Height	<0.0001	-0.9176	2.4629
	Stem form	<0.0001	-0.6398	0.8622
1010802EA62A3	DBH	0.3242	-0.1571	0.1127
	Height	<0.0001	-0.5216	1.6113
	Stem form	0.0002	0.0812	-0.2502
1010802EA62A4	DBH	0.2584	0.0575	0.2769
	Height	<0.0001	-1.4111	7.2478
	Stem form	<0.0001	0.0755	0.8157
1010802EA62A5	DBH	<0.0001	-0.3284	1.7270
	Height	0.0022	-0.2182	0.5398
	Stem form	<0.0001	0.1940	-0.1900
1010802EA62A6	DBH	0.0099	-0.3715	0.7306
	Height	0.0025	-0.2275	0.4597
	Stem form	<0.0001	-0.4468	0.7409

Table 4.2 Normality of residuals test statistics for the F_3 *E. grandis* trials.

Trial	**Trait**	**Normality of distribution test statistics**					
		Shapiro-Wilk Pr < W		**Skewness**		**Kurtosis**	
		Dukuduku	Silverfontein	Dukuduku	Silverfontein	Dukuduku	Silverfontein
1010802EA62B4	DBH	<0.0001	<0.0001	-0.8490	-0.8056	0.8910	0.7342
	Height	<0.0001	<0.0001	-1.5840	-0.8800	3.6839	0.9448
	Stem form	<0.0001	0.0004	-1.1631	-0.2518	2.2267	0.7501
1010802EA62B5	DBH	<0.0001	<0.0001	-0.9552	-0.6141	1.0398	0.6287
	Height	<0.0001	<0.0001	-1.8424	-1.3379	4.7710	2.8937
	Stem form	<0.0001	<0.0001	-1.4146	-0.6569	3.1521	0.6010
1010802EA62B6	DBH	<0.0001	<0.0001	-0.7425	-0.7150	0.4251	0.5956
	Height	<0.0001	<0.0001	-1.4984	-1.0618	3.1962	2.5241
	Stem form	<0.0001	<0.0001	-1.1338	-0.3152	1.7778	0.4991
1010802EA62B7	DBH	<0.0001	<0.0001	-0.6523	-0.9020	0.5504	0.8903
	Height	<0.0001	<0.0001	-1.1009	-1.6905	2.4810	4.7223
	Stem form	<0.0001	<0.0001	-0.9856	-0.5108	1.5435	0.8972
1010802EA62B8	DBH	<0.0001	<0.0001	-0.8399	-0.6855	1.1845	0.7132
	Height	<0.0001	<0.0001	-1.5235	-1.3569	4.6239	2.8449
	Stem form	<0.0001	<0.0001	-0.8573	-0.4612	1.2202	1.1568
1010802EA62B9	DBH	<0.0001	<0.0001	-0.734	-0.7398	0.8486	0.5801
	Height	<0.0001	<0.0001	-1.5451	-0.9080	5.0771	1.5390
	Stem form	<0.0001	0.0032	-0.7642	-0.0073	0.7203	0.2388
1010802EA62B10	DBH	<0.0001	<0.0001	-0.5623	-0.6567	0.0368	1.1604
	Height	<0.0001	<0.0001	-0.7740	-1.5172	0.7470	4.1495
	Stem form	<0.0001	<0.0001	-0.4823	-0.4641	0.1939	0.7084

Trial	Trait	Normality of distribution test statistics					
		Shapiro-Wilk Pr < W		Skewness		Kurtosis	
1010802EA62B11	DBH	<0.0001	<0.0001	-0.7403	-0.5405	0.6883	0.4019
	Height	<0.0001	<0.0001	-0.8062	-1.0779	1.7364	1.9837
	Stem form	<0.0001	<0.0001	-0.4568	-0.4978	0.1640	0.6470
1010802EA62B12	DBH	0.0007	<0.0001	-0.3241	-0.4666	-0.0604	-0.0835
	Height	<0.0001	<0.0001	-0.4709	-0.8898	0.6005	1.0342
	Stem form	0.0004	<0.0001	-0.2756	-0.6356	0.1031	0.5435
1010802EA62B13	DBH	<0.0001	<0.0001	-0.4567	-0.4756	0.0199	0.0958
	Height	<0.0001	<0.0001	-0.7905	-1.0386	0.6503	1.8830
	Stem form	<0.0001	<0.0001	-0.4576	-0.5274	0.4964	0.4064
1010802EA62B14	DBH	<0.0001	<0.0001	-0.8490	-0.7262	0.8910	0.9067
	Height	<0.0001	<0.0001	-1.5840	-1.4438	3.6839	3.7835
	Stem form	<0.0001	<0.0001	-1.1631	-0.4018	2.2266	0.0870
1010802EA62B15	DBH	<0.0001	<0.0001	-0.7948	-0.8733	0.5156	1.4907
	Height	<0.0001	<0.0001	-1.5039	-0.8938	2.9129	0.0860
	Stem form	<0.0001	<0.0001	-1.0153	-0.5534	1.3627	0.3672
1010802EA62B16	DBH	<0.0001	<0.0001	-0.7761	-0.8279	0.4816	1.5381
	Height	<0.0001	<0.0001	-1.3313	-0.7220	2.3043	0.9872
	Stem form	<0.0001	<0.0001	-1.0773	-0.5340	1.5427	0.3438

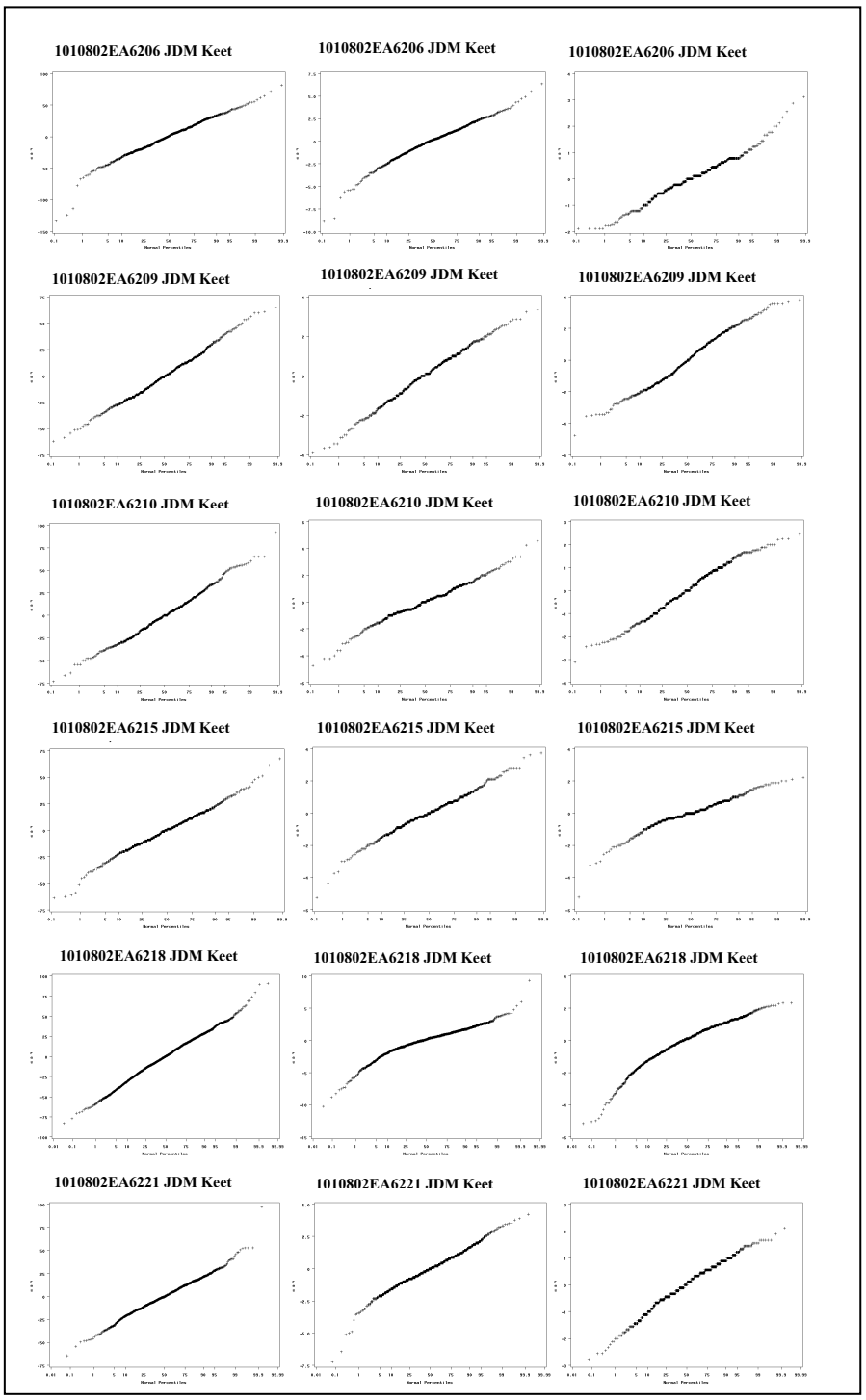

Figure 4.1 Normal probability plots for each trait in the F_1 *E. grandis* trials.

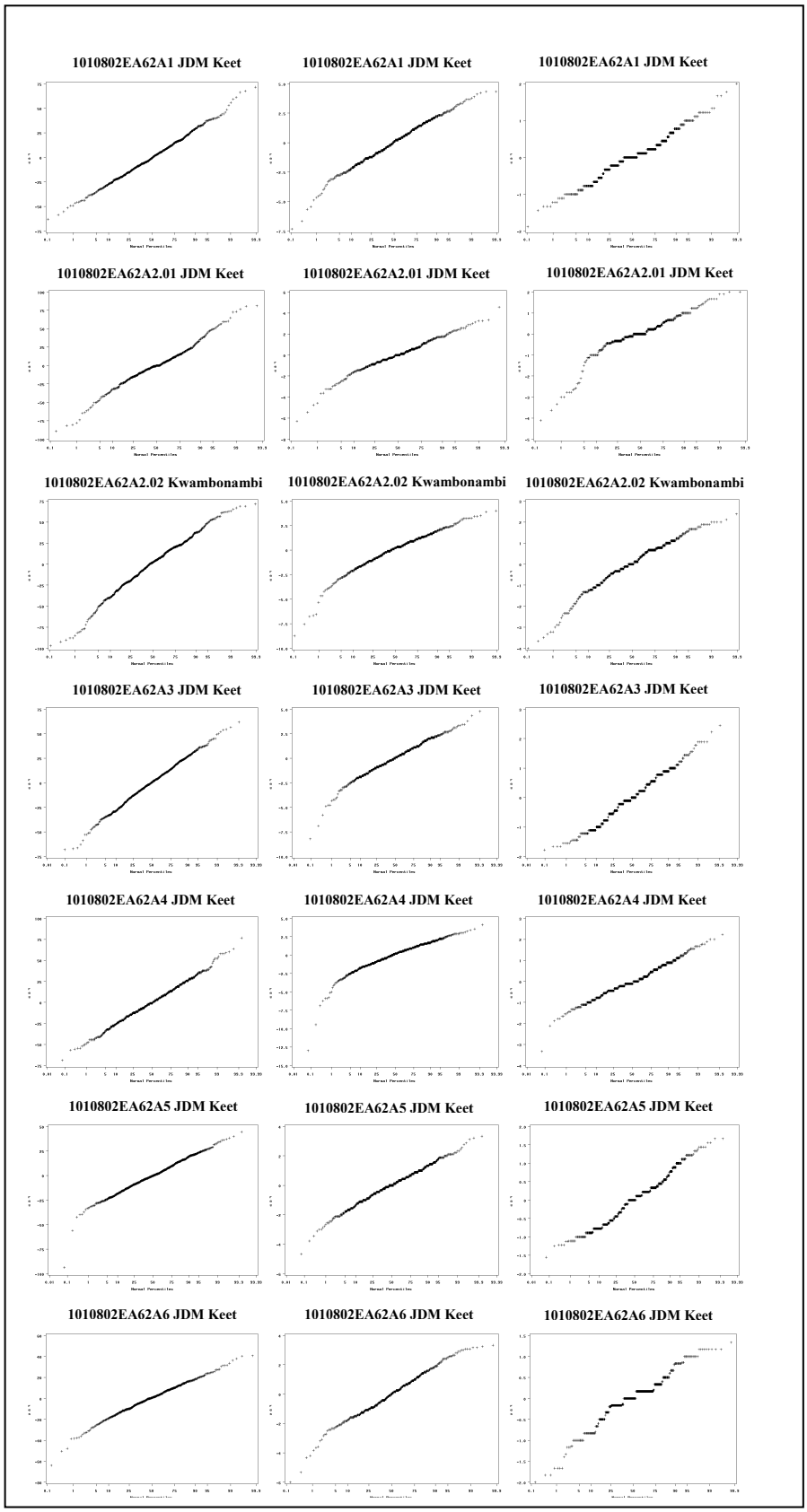

Figure 4.2 Normal probability plots for each trait in the F_2 *E. grandis* trials.

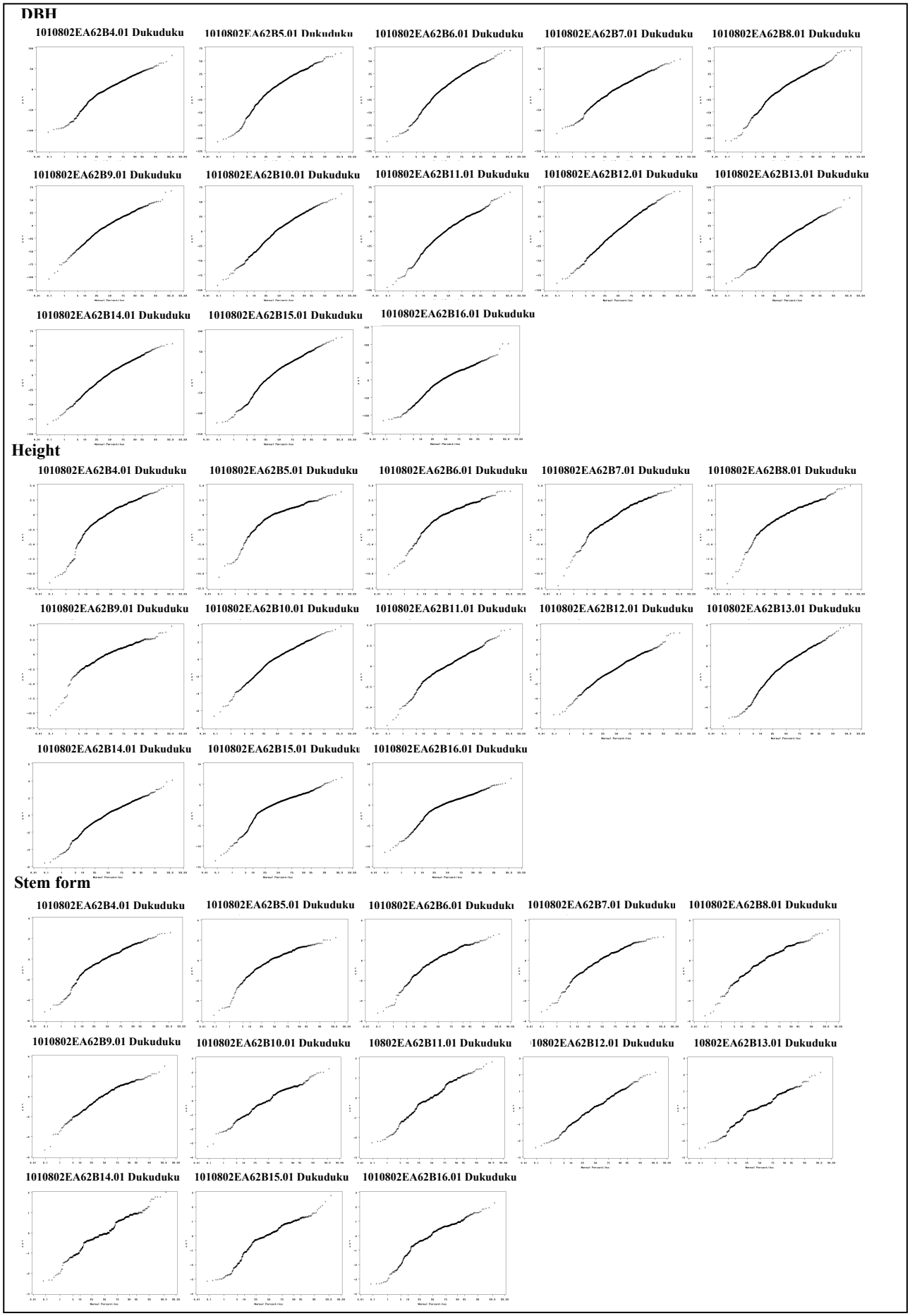

Figure 4.3 Normal probability plots for each trait in the F_3 *E. grandis* trials at Dukuduku plantation.

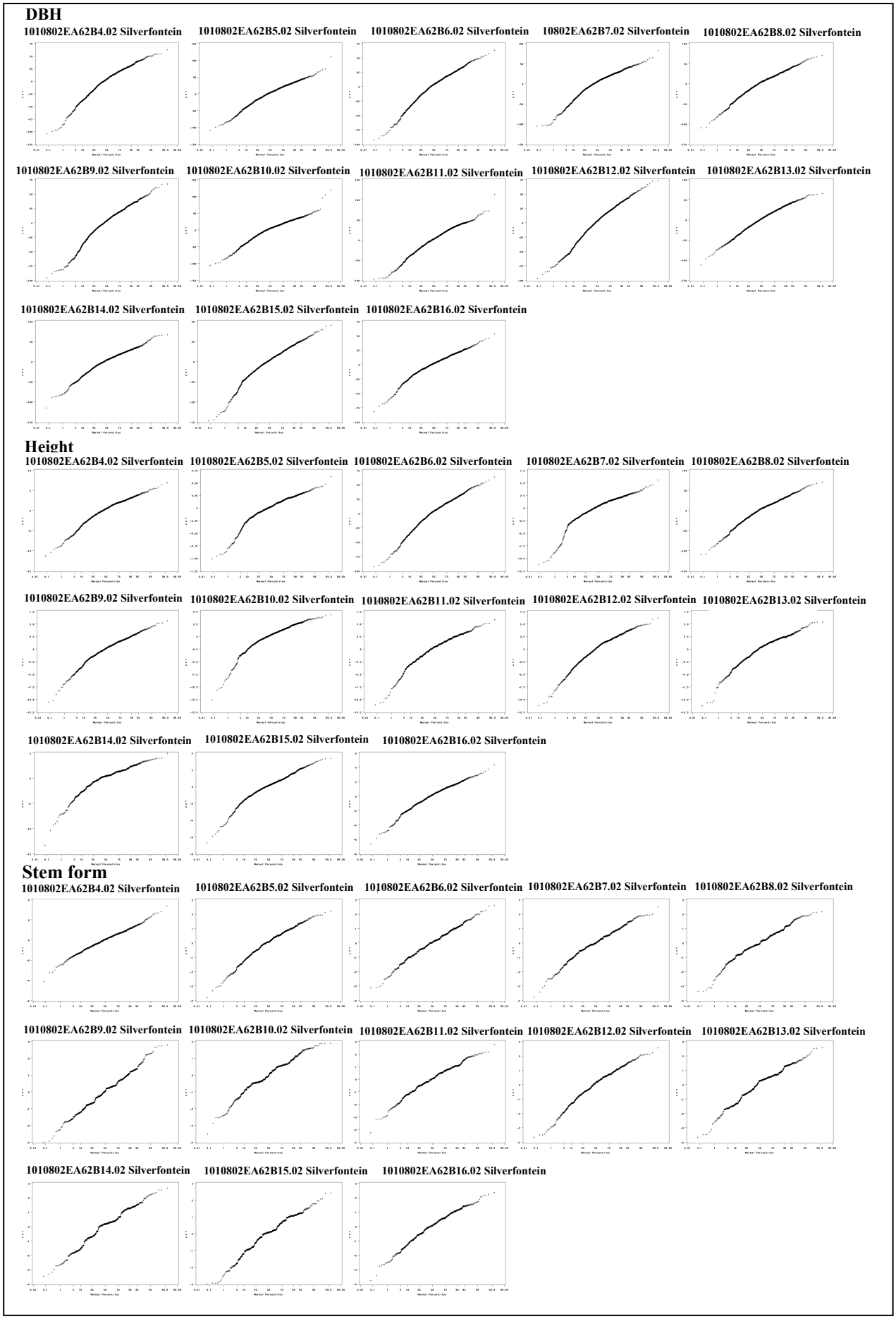

Figure 4.4 Probability normal plots for each trait in the F_3 *E. grandis* trials at Silverfontein plantation.

4.2.2 Significance of family effects

An analysis of variance (ANOVA) was done for each trait in all the trials using the PROC GLM procedure in SAS to test for the significance of family effects.

At the 5% level of significance ($\alpha = 0.05$), DBH and height family effects were significant in all of the F_1 trials and for stem form in all trials except for 1010802EA6215 (Table 4.3). The family effect for DBH in F_2 trial 1010802EA62A2.01 (J.D.M. Keet plantation) and stem form in F_2 trial 1010802EA62A6 were not significant at $\alpha = 0.05$ (Table 4.4). All the remaining F_2 trials had significant family effects for DBH, height and stem form (Table 4.4). All of the F_3 trials had significant family effects for all three traits at the 5% level of significance (Table 4.5 and Table 4.6).

Table 4.3 Analysis of variance for significance of family effects in the F_1 *E. grandis* trials.

Trial	Trait	DF	F Value	Pr > F
1010802EA6206	DBH		2.15	< 0.0001
	Height	59	1.59	0.0049
	Stem		1.84	0.0003
1010802EA6209	DBH		1.68	0.0020
	Height	60	2.45	< 0.0001
	Stem		1.47	0.0167
1010802EA6210	DBH		1.71	0.0015
	Height	59	2.64	< 0.0001
	Stem		1.70	0.0016
1010802EA6215	DBH		1.41	0.0312
	Height	58	1.90	0.0002
	Stem		1.30	0.0807
1010802EA6218	DBH		2.77	< 0.0001
	Height	98	3.13	< 0.0001
	Stem		2.10	< 0.0001
1010802EA6221	DBH		2.18	< 0.0001
	Height	98	2.22	< 0.0001
	Stem		1.50	0.0023

*Families were removed from EA6206, EA6209, EA6209 and EA6215 at two years based on poor performance and mortality rates within those families.

Table 4.4 Analysis of variance for significance of family effects in the F_2 *E. grandis* trials.

Trial	Trait	DF	F Value	Pr > F
1010802EA62A1	DBH	63	2.22	< 0.0001
	Height		2.09	< 0.0001
	Stem		1.66	0.0017
1010802EA62A2.01	DBH	63	1.34	0.0599
(J.D.M. Keet)	Height		1.72	0.0018
	Stem		1.48	0.0194
1010802EA62A2.02	DBH	63	2.51	< 0.0001
(Kwambonambi)	Height		2.56	< 0.0001
	Stem		1.77	0.0005
1010802EA62A3	DBH	71	1.99	< 0.0001
	Height		1.76	0.0003
	Stem		1.59	0.0025
1010802EA62A4	DBH	98	1.77	< 0.0001
	Height		1.39	0.0102
	Stem		1.54	0.0012
1010802EA62A5	DBH	98	1.97	< 0.0001
	Height		1.52	0.0017
	Stem		1.70	< 0.0001
1010802EA62A6	DBH	71	1.60	0.0032
	Height		1.64	0.0019
	Stem		1.17	0.1830

Table 4.5 Analysis of variance for significance of family effects in the F_3 *E. grandis* trials at Dukuduku plantation.

Trial	Trait	DF	F Value	Pr > F
1010802EA62B4.01	DBH		2.48	< 0.0001
	Height	49	2.45	< 0.0001
	Stem		2.02	< 0.0001
1010802EA62B5.01	DBH		1.81	0.0008
	Height	49	1.41	0.0381
	Stem		1.44	0.0279
1010802EA62B6.01	DBH		1.85	0.0005
	Height	49	1.69	0.0027
	Stem		1.83	0.0007
1010802EA62B7.01	DBH		2.26	< 0.0001
	Height	49	1.95	0.0002
	Stem		1.92	0.0003
1010802EA62B8.01	DBH		3.10	< 0.0001
	Height	49	2.80	< 0.0001
	Stem		2.53	< 0.0001
1010802EA62B9.01	DBH		3.53	< 0.0001
	Height	49	3.81	< 0.0001
	Stem		3.42	< 0.0001
1010802EA62B10.01	DBH		3.70	< 0.0001
	Height	49	3.26	< 0.0001
	Stem		2.23	< 0.0001
1010802EA62B11.01	DBH		1.64	0.0045
	Height	49	1.63	0.0051
	Stem		1.71	0.0023
1010802EA62B12.01	DBH		3.10	< 0.0001
	Height	49	3.06	< 0.0001
	Stem		2.78	< 0.0001
1010802EA62B13.01	DBH		1.96	0.0002
	Height	49	3.20	< 0.0001
	Stem		1.85	0.0005
1010802EA62B14.01	DBH		2.66	< 0.0001
	Height	49	2.41	< 0.0001
	Stem		1.85	< 0.0001
1010802EA62B15.01	DBH		2.38	< 0.0001
	Height	49	2.29	< 0.0001
	Stem		2.06	< 0.0001
1010802EA62B16.01	DBH		2.65	< 0.0001
	Height	49	2.65	< 0.0001
	Stem		2.32	< 0.0001

Table 4.6 Analysis of variance for significance of family effects in the F_3 *E. grandis* trials at Silverfontein plantation.

Trial	Trait	DF	F Value	Pr > F
1010802EA62B4.02	DBH	49	3.12	< 0.0001
	Height		2.52	< 0.0001
	Stem		3.23	< 0.0001
1010802EA62B5.02	DBH	49	2.97	< 0.0001
	Height		2.76	< 0.0001
	Stem		3.74	< 0.0001
1010802EA62B6.02	DBH	49	2.35	< 0.0001
	Height		1.92	0.0002
	Stem		3.59	< 0.0001
1010802EA62B7.02	DBH	49	2.22	< 0.0001
	Height		1.91	0.0003
	Stem		2.52	< 0.0001
1010802EA62B8.02	DBH	49	2.92	< 0.0001
	Height		2.33	< 0.0001
	Stem		3.04	< 0.0001
1010802EA62B9.02	DBH	49	1.90	0.0003
	Height		1.95	0.0002
	Stem		1.82	0.0007
1010802EA62B10.02	DBH	49	1.47	0.0212
	Height		1.60	0.0068
	Stem		1.95	0.0002
1010802EA62B11.02	DBH	49	2.33	< 0.0001
	Height		2.20	< 0.0001
	Stem		2.27	< 0.0001
1010802EA62B12.02	DBH	49	1.60	0.0063
	Height		2.01	< 0.0001
	Stem		1.74	0.0016
1010802EA62B13.02	DBH	49	1.80	0.0008
	Height		2.23	< 0.0001
	Stem		1.92	0.0002
1010802EA62B14.02	DBH	49	2.09	< 0.0001
	Height		1.76	0.0013
	Stem		1.51	0.0150
1010802EA62B15.02	DBH	49	2.83	< 0.0001
	Height		2.89	< 0.0001
	Stem		2.33	< 0.0001
1010802EA62B16.02	DBH	49	3.29	< 0.0001
	Height		2.81	< 0.0001
	Stem		2.74	< 0.0001

4.3 Estimation of genetic parameters

4.3.1 Estimation of variance components and narrow-sense heritability

Variance components and narrow-sense heritabilities were estimated for each trait in all the F_1, F_2 and F_3 *E. grandis* trials. These estimates were then used for the estimation of BLUP selection indices.

The variance and covariance component estimates required for the calculation of narrow-sense heritabilities were estimated in each trial with Harvey's Mixed Model Least-Squares and Maximum Likelihood programme. The family component of variance (σ_f^2) and the environmental (error) component of variance (σ_e^2) for each trial are presented in Table 4.7, Table 4.8 and Table 4.9. The among family covariance components and the error variance estimates between the three selection traits in each trial are presented in Table A1 to Table A4 in Appendix A.

Table 4.7 Family and environmental variance component estimates in the F_1 *E. grandis* trials.

	DBH		**Height**		**Stem form**	
Trial	σ_f^2	σ_e^2	σ_f^2	σ_e^2	σ_f^2	σ_e^2
1010802EA6206	0.1258	0.8442	0.08411	0.8822	0.0715	0.7415
1010802EA6209	0.0606	0.8849	0.1457	0.7721	0.0499	0.8756
1010802EA6210	0.0754	0.8750	0.1507	0.7647	0.0676	0.8164
1010802EA6215	0.0435	0.8945	0.0920	0.8131	0.0337	0.8145
1010802EA6218	0.0893	0.8986	0.1086	0.8343	0.0586	0.8310
1010802EA6221	0.1120	0.8654	0.1247	0.8033	0.0401	0.7944

Table 4.8 Family and environmental variance component estimates in the F_2 *E. grandis* trials.

Trial	DBH		Height		Stem form	
	σ_f^2	σ_e^2	σ_f^2	σ_e^2	σ_f^2	σ_e^2
1010802EA62A1	0.1132	0.8553	0.0946	0.8265	0.0491	0.6838
1010802EA62A2.01 J.D.M. Keet	0.0471	0.9086	0.1066	0.8005	0.0725	0.6922
1010802EA62A2.02 Kwambonambi	0.1445	0.8242	0.1527	0.7778	0.0806	0.7930
1010802EA62A3	0.0837	0.8875	0.0722	0.8531	0.0522	0.7759
1010802EA62A4	0.0777	0.8788	0.0548	0.8664	0.0449	0.7506
1010802EA62A5	0.0964	0.8803	0.0509	0.8408	0.0512	0.6743
1010802EA62A6	0.0898	0.8808	0.0929	0.8639	0.0250	0.6406

Table 4.9 Family and environmental variance component estimates in the F_3 *E. grandis* trials at Dukuduku and Silverfontein plantations.

Site	Trial	DBH		Height		Stem form	
		σ_f^2	σ_e^2	σ_f^2	σ_e^2	σ_f^2	σ_e^2
Dukuduku	1010802EA62B4.01	0.0873	0.8701	0.0863	0.8274	0.0548	0.8065
	1010802EA62B5.01	0.0513	0.9031	0.0354	0.8390	0.0371	0.8057
	1010802EA62B6.01	0.0681	0.8863	0.0559	0.8335	0.0470	0.8120
	1010802EA62B7.01	0.0816	0.8725	0.0687	0.8313	0.0614	0.8069
	1010802EA62B8.01	0.1208	0.8369	0.1074	0.8079	0.0740	0.7937
	1010802EA62B9.01	0.1409	0.8080	0.1442	0.7442	0.1165	0.7411
	1010802EA62B10.01	0.1345	0.8210	0.1170	0.8376	0.0553	0.7634
	1010802EA62B11.01	0.0569	0.8955	0.0568	0.8943	0.0415	0.7466
	1010802EA62B12.01	0.1159	0.8368	0.1190	0.8330	0.0842	0.7134
	1010802EA62B13.01	0.0695	0.8843	0.1442	0.8092	0.0431	0.7418
	1010802EA62B14.01	0.0945	0.8635	0.0874	0.8700	0.0408	0.7096
	1010802EA62B15.01	0.0763	0.8831	0.0825	0.8760	0.0471	0.7575
	1010802EA62B16.01	0.0864	0.8725	0.0885	0.8699	0.0595	0.7490

Site	Trial	DBH		Height		Stem form	
		σ_f^2	σ_e^2	σ_f^2	σ_e^2	σ_f^2	σ_e^2
Silverfontein	1010802EA62B4.02	0.1120	0.8542	0.1081	0.8534	0.1183	0.7380
	1010802EA62B5.02	0.0943	0.8642	0.0864	0.8313	0.1088	0.7380
	1010802EA62B6.02	0.0748	0.8835	0.0465	0.9116	0.1184	0.7346
	1010802EA62B7.02	0.0724	0.8863	0.0590	0.8511	0.0697	0.7654
	1010802EA62B8.02	0.0814	0.8766	0.0655	0.8487	0.0856	0.7457
	1010802EA62B9.02	0.0357	0.9220	0.0425	0.9098	0.0415	0.7974
	1010802EA62B10.02	0.0348	0.9310	0.0414	0.8816	0.0496	0.7663
	1010802EA62B11.02	0.0659	0.8930	0.0625	0.8648	0.0573	0.8046
	1010802EA62B12.02	0.0437	0.9152	0.0609	0.8598	0.0428	0.8216
	1010802EA62B13.02	0.0411	0.9190	0.0683	0.8539	0.0405	0.8034
	1010802EA62B14.02	0.0596	0.9002	0.0496	0.8691	0.0176	0.8444
	1010802EA62B15.02	0.0728	0.8878	0.0841	0.8757	0.0527	0.7868
	1010802EA62B16.02	0.1025	0.8547	0.0898	0.8669	0.0754	0.7614

The narrow-sense heritability estimates for DBH, height and stem form in each of the F_1, F_2 and F_3 *E. grandis* trials were calculated with Harvey's Mixed Model Least-Squares and Maximum Likelihood programme (Table 4.10, Table 4.11 and Table 4.12). Heritabilities ranged from 0.155 to 0.432 for DBH in the F_1 trials, 0.164 to 0.497 in the F_2 trials and from 0.120 to 0.495 in the F_3 trials. Height heritability ranged from 0.290 to 0.549 in the F_1 trials, 0.190 to 0.547 in the F_2 trials and from 0.135 to 0.541 in the F_3 trials. Stem form heritability ranged from 0.132 to 0.293 in the F_1 trials, 0.125 to 0.316 in the F_2 trials and from 0.068 to 0.463 in the F_3 trials.

Table 4.10 Narrow-sense heritability estimates for selection traits in the F_1 *E. grandis* trials.

Trial	DBH		Height		Stem form	
	h^2	std error	h^2	std error	h^2	std error
1010802EA6206	0.432	0.130	0.290	0.114	0.293	0.115
1010802EA6209	0.214	0.108	0.529	0.143	0.180	0.104
1010802EA6210	0.265	0.114	0.549	0.145	0.255	0.113
1010802EA6215	0.155	0.101	0.339	0.124	0.132	0.098
1010802EA6218	0.301	0.064	0.384	0.072	0.220	0.055
1010802EA6221	0.382	0.096	0.448	0.102	0.160	0.075

Table 4.11 Narrow-sense heritability estimates for selection traits in the F_2 *E. grandis* trials.

Trial	DBH		Height		Stem form	
	h^2	std error	h^2	std error	h^2	std error
1010802EA62A1	0.390	0.120	0.342	0.115	0.223	0.101
1010802EA62A2.01 J.D.M. Keet	0.164	0.135	0.392	0.159	0.316	0.151
1010802EA62A2.02 Kwambonambi	0.497	0.133	0.547	0.137	0.307	0.112
1010802EA62A3	0.287	0.103	0.260	0.099	0.210	0.094
1010802EA62A4	0.271	0.086	0.198	0.079	0.188	0.078
1010802EA62A5	0.329	0.092	0.190	0.078	0.235	0.083
1010802EA62A6	0.308	0.138	0.324	0.139	0.125	0.119

Table 4.12 Narrow-sense heritability estimates for selection traits in the F_3 *E. grandis* trials at Dukuduku and Silverfontein plantations.

Site	Trial	DBH		Height		Stem form	
		h^2	std error	h^2	std error	h^2	std error
Dukduku	1010802EA62B4.01	0.304	0.095	0.315	0.096	0.212	0.081
	1010802EA62B5.01	0.179	0.077	0.135	0.69	0.147	0.071
	1010802EA62B6.01	0.238	0.088	0.210	0.084	0.182	0.079
	1010802EA62B7.01	0.285	0.096	0.254	0.092	0.236	0.089
	1010802EA62B8.01	0.420	0.109	0.391	0.105	0.284	0.090
	1010802EA62B9.01	0.495	0.126	0.541	0.132	0.453	0.121
	1010802EA62B10.01	0.469	0.117	0.409	0.109	0.225	0.082
	1010802EA62B11.01	0.199	0.083	0.199	0.083	0.176	0.079
	1010802EA62B12.01	0.406	0.114	0.417	0.115	0.352	0.106
	1010802EA62B13.01	0.243	0.088	0.504	0.124	0.183	0.078
	1010802EA62B14.01	0.329	0.095	0.304	0.091	0.181	0.072
	1010802EA62B15.01	0.265	0.085	0.287	0.088	0.195	0.074
	1010802EA62B16.01	0.300	0.090	0.308	0.091	0.245	0.082
Silverfontein	1010802EA62B4.02	0.386	0.107	0.375	0.105	0.460	0.117
	1010802EA62B5.02	0.328	0.094	0.314	0.092	0.428	0.108
	1010802EA62B6.02	0.260	0.085	0.162	0.069	0.463	0.114
	1010802EA62B7.02	0.252	0.082	0.216	0.077	0.278	0.086
	1010802EA62B8.02	0.283	0.088	0.239	0.081	0.343	0.097

Site	Trial	DBH		Height		Stem form	
		h^2	std error	h^2	std error	h^2	std error
Silverfontein	1010802EA62B9.02	0.124	0.063	0.149	0.067	0.165	0.070
	1010802EA62B10.02	0.120	0.063	0.150	0.068	0.203	0.076
	1010802EA62B11.02	0.229	0.079	0.225	0.078	0.221	0.078
	1010802EA62B12.02	0.152	0.066	0.221	0.078	0.165	0.069
	1010802EA62B13.02	0.143	0.063	0.247	0.080	0.160	0.066
	1010802EA62B14.02	0.207	0.075	0.180	0.071	0.068	0.052
	1010802EA62B15.02	0.253	0.081	0.292	0.087	0.209	0.074
	1010802EA62B16.02	0.357	0.099	0.313	0.093	0.300	0.091

4.3.2 Phenotypic correlation between selection traits

The phenotypic correlation between the selection traits, DBH, height and stem form, in the trials used for forward prediction was calculated in SAS. The Pearson correlation coefficients between these traits for each F_1 trial, for the F_1 combined set of trials, for each F_2 trial and the F_2 combined set of trials are presented in Table 4.13. The correlation coefficients were highest between DBH and height. All correlations (except for one in trial 1010802EA6206) were significant at the $\alpha = 0.05$ level of significance.

Table 4.13 Pearson correlation coefficients between selection traits in the F_1 and F_2 *E. grandis* trials.

Generation	Trial	n	Phenotypic Correlations		
			DBH-Height	DBH-Stem form	Height-Stem form
F_1 *E. grandis*	1010802EA6206	530	0.55225^{***}	-0.09593^{*}	-0.05461^{ns}
	1010802EA6209	509	0.53642^{***}	0.29564^{***}	0.20255^{***}
	1010802EA6210	507	0.59495^{***}	0.24020^{***}	0.27826^{***}
	1010802EA6215	500	0.71262^{***}	0.21856^{***}	0.14371^{**}
	1010802EA6218	1727	0.77326^{***}	0.32405^{***}	0.33856^{***}
	1010802EA6221	884	0.72716^{***}	0.46353^{***}	0.37390^{***}
Combined F_1 *E. grandis* trials		4657	0.68862^{***}	0.28094^{***}	0.25936^{***}

Generation	Trial	n	Phenotypic Correlations		
			DBH-Height	DBH-Stem form	Height-Stem form
F_2 *E. grandis*	1010802EA62A1	576	0.62848***	0.25444***	0.1342**
	1010802EA62A2.01 J.D.M. Keet	363	0.50724***	0.23379***	0.10849*
	1010802EA62A2.02 Kwambonambi	566	0.73312***	0.35082***	0.33503***
	1010802EA62A3	647	0.71647***	0.26924***	0.18816***
	1010802EA62A4	878	0.58357***	0.17978***	0.21004***
	1010802EA62A5	875	0.64906***	0.22055***	0.18971***
	1010802EA62A6	427	0.56658***	0.24870***	0.27436***
Combined F_2 *E. grandis* trials		4332	0.63427***	0.24566***	0.20785***

Correlation coefficient significant effect: *** p<0.0001 ** p<0.01 * p<0.05 ns non-significant at p = 0.05

4.4 Predicted breeding values

Individual performance within the F_1 and F_2 *E. grandis* population data were predicted by means of forward prediction BLUP breeding values. Multiple-site, multiple-trait analyses were run in Matgen using the forward selection model (as described in section 3.5.4). Four scenarios, one for each of the different matrix inversion techniques and adapted ridge regression were run in the higher precision (Delphi) Matgen algorithm. Two scenarios, were run in the lower precision (Clipper) Matgen programme where only two different matrix inversion techniques (the two Gaussian elimination methods) were available. There were 10 runs (one for each set of economic weightings as given in Table 3.1) per scenario and these were run in turn for each generation of trials. Single-trait, multiple-site scenarios were also run in Delphi Matgen and in Clipper Matgen and compared to the multiple-site multiple-trait scenarios. Ridge regression was not applied as a collinearity mitigation method for the single-trait scenarios, as these models are simpler and less likely to display collinearity.

4.4.1 The choice of k values for adapted ridge regression

The k values that were used for the adapted ridge regression runs were estimated (using the methods described in section 3.5.3) based on the data and also thus varied for the different data sets in this study. Values for k in the F_1 trials were either zero (where no collinearity effect was present) or 0.1 for each family. In the F_2 trials ridge regression runs the k values that were used for each family were either zero or ranged from 0.01 to 0.08 (in increments of 0.01; here there was varying severity of the collinearity effects).

4.4.2 Instability

The output from the Matgen programmes lists the heritabilities of the selection traits for each site, the among family and within family variances and covariances and the BLUP ranks of each individual in the population data (forward prediction runs) or BLUP ranks for each parent of a family in the population data (backward prediction runs). An indication of the instability (as described in 3.5.5) is given in the output as the total number of unstable cases found and these are marked in the rank list by asterisks.

In the forward prediction runs in the F_1 trial data set, varying the economic weights had an effect on the number of cases of instability detected in the data set by Matgen. Most cases of instability were observed when more weight was placed on the stem form trait.

The levels of instability and where it occurs in the F_1 *E. grandis* analyses is described in Table 4.14. The partial pivoting matrix inversion method and the adapted ridge regression scenarios had the most unstable cases indicated in the high precision programme (ranged in instability in individuals from three (0.69%) families to 63 (14.6%) families). Both full pivoting and singular value decomposition matrix inversion methods indicated very few cases of instability. The lower precision Clipper versions of the programme presented a substantially higher number of unstable cases (ranging in instability in individuals from 59 (13.6%) families to individuals from 373 (86.5%) families and one case where there was instability in all 431 families) than in the higher precision Delphi programme (as stated above, this ranged from individuals from a single family to instability in individuals from 63 families across the different inversion techniques) in the F_1 *E. grandis* data set.

Table 4.14 Instability levels detected in the F_1 *E. grandis* forward selection runs in Matgen.

Economic weighting set No.	Number of instability cases detected by Matgen	Forward prediction method					
		PP	FP	SVD	RIDGE	Low PP	Low FP
1	Families	3	1	1	3	63	59
	Individuals	27	1	1	36	572	527
2	Families	3	1	1	3	313	312
	Individuals	27	1	1	36	3644	3644
3	Families	3	1	1	4	313	312
	Individuals	27	1	1	45	3644	3644
4	Families	3	1	1	4	373	372
	Individuals	27	1	1	45	4151	4143
5	Families	3	1	1	4	218	217
	Individuals	27	1	1	45	2795	2795
6	Families	63	1	1	63	372	181
	Individuals	566	1	1	566	4165	1893
7	Families	63	1	1	63	122	121
	Individuals	539	1	1	557	1110	1074
8	Families	3	1	1	3	218	217
	Individuals	27	1	1	36	2778	2769
9	Families	3	1	1	4	218	217
	Individuals	27	1	1	45	2795	2790
10	Families	63	1	1	63	431	431
	Individuals	566	1	1	566	4672	4672

Total number of families in the F_1 runs was 431

Total number of individuals in the F_1 runs was 4672

PP = partial pivoting high precision control; FP = full pivoting high precision; SVD = singular value decomposition; RIDGE = adapted ridge regression; low PP = partial pivoting low precision in Clipper Matgen; low FP = full pivoting low precision in Clipper Matgen

*For a description on the economic weighting sets please refer to Table 3.1.

Indicators of instability in the forward prediction methods:

- Wrong sign coefficients and high correlations between predicted and true values
- Very large condition numbers observed (condition numbers are used in the SVD runs)
- In the inversions of the V matrix where values may be too large or too small and cause problems in the inversion
- Examining the matrix calculated from the product of the phenotypic covariance matrix with its inverse, for deviations from the expected identity pattern

In the forward prediction runs in the F_2 *E. grandis* trial data set the same effect on the number of cases of instability detected by Matgen when varying the economic weights was observed. The levels of instability and where it occurs is described in Table 4.15. The partial pivoting matrix inversion method and the adapted ridge regression scenarios in the high precision programme once again had the most unstable cases indicated (ranged in instability in individuals from 72 (15.5%) families to individuals from 122 (26.2%) families and individuals from 61 (13.1%) to 122 (26.2%) families respectively out of a total of 466 families). Both full pivoting and singular value decomposition matrix inversion methods indicated far fewer cases of instability as shown in Table 4.15. The lower precision Clipper versions of the programme also indicated a substantially higher number of unstable individuals as found in the F_1 *E. grandis* data set (ranging in instability in individuals from 61 (13.1%) family to instability in individuals from 270 (57.9%) families) in comparison to the higher precision Delphi programme (where the overall range was from instability in individuals from 13 (2.8%) families to instability in individuals from 122 (26.2%) families across the different inversion techniques) in the F_2 *E. grandis* data set.

Table 4.15 Instability levels detected in the F_2 *E. grandis* forward selection runs in Matgen.

Economic weighting set No.	**Number of instability cases detected by Matgen**	**Forward prediction method**					
		PP	**FP**	**SVD**	**RIDGE**	**Low PP**	**Low FP**
1	Families	95	13	13	74	105	61
	Individuals	718	13	13	553	795	540
2	Families	122	13	13	62	124	62
	Individuals	903	13	13	371	943	921
3	Families	72	13	13	71	66	61
	Individuals	461	13	13	452	421	363
4	Families	107	13	13	118	109	61
	Individuals	769	13	13	903	800	769
5	Families	95	13	13	74	207	163
	Individuals	718	13	13	553	1698	1461
6	Families	122	13	13	122	268	206
	Individuals	903	13	13	903	2009	1995

Economic weighting set No.	Number of instability cases detected by Matgen	Forward prediction method PP	FP	SVD	RIDGE	Low PP	Low FP
7	Families	95	13	13	61	194	133
	Individuals	718	13	13	540	1564	1550
8	Families	95	13	13	74	107	62
	Individuals	718	13	13	553	821	558
9	Families	95	13	13	74	224	165
	Individuals	718	13	13	553	1820	1816
10	Families	122	13	13	120	270	209
	Individuals	903	13	13	903	2025	2029

Total number of families in the F_2 runs was 466
Total number of individuals in the F_2 runs was 4332

PP = partial pivoting high precision control; FP = full pivoting high precision; SVD = singular value decomposition; RIDGE = adapted ridge regression; low PP = partial pivoting low precision in Clipper Matgen; low FP = full pivoting low precision in Clipper Matgen

*For a description on the economic weighting sets please refer to Table 3.1.

Indicators of instability in the forward prediction methods:

- Wrong sign coefficients and high correlations between predicted and true values
- Very large condition numbers observed (condition numbers are used in the SVD runs)
- In the inversions of the V matrix where values may be too large or too small and cause problems in the inversion
- Examining the matrix calculated from the product of the phenotypic covariance matrix with its inverse, for deviations from the expected identity pattern

4.4.3 The effect of instability on population parameters

The standard deviations of the predicted breeding values ($\hat{g}_{fwd}$) were calculated in SAS and the mean values across methods were mostly found to be the lowest in the relatively stable *E. grandis* F_1 population scenarios (Table A7 in Appendix A). The mean standard deviation values among techniques ranged from 0.231 to 0.347 across economic weighting scenarios in the F_1 population data. The standard deviations were higher in most cases in the F_2 *E. grandis* population data which were less stable. Standard deviations ranged from 0.315 to 3.839 in the F_2 *E. grandis* scenarios.

The measures of deviation from normality of $\hat{g}_{fwd}$ (e.g. kurtosis and skewness) followed a similar pattern of increase as the population became less stable (Table A7 in Appendix A). Kurtosis and skewness values were much closer to the expected zero level of normally distributed population data in the F_1 *E. grandis* scenarios (values as low as 0.001 in some techniques). In the less stable F_2 *E. grandis* population data these values were much higher (kurtosis ranged from 3.58 to 32.08).

4.5 Realised breeding performance

Realised breeding performance, the performance of the parents in the next generation, was estimated by backward prediction in the F_2 and F_3 *E. grandis* trials. Scenarios were run in Matgen (Delphi – higher precision) with partial pivoting, full pivoting and singular value decomposition (SVD) matrix inversion techniques for each economic weighting set. Runs were also completed in the Clipper (lower precision) version of Matgen. The Pearson correlation coefficients between the Clipper and the Delphi backward predictions runs in Matgen were $r = 1$ ($p < 0.0001$) in the F_2 trials and therefore only the Delphi runs were used further in the study. The Clipper and Delphi backward prediction runs in the F_3 trials had correlation coefficients close to $r = 1$ ($p < 0.0001$) and the Delphi backward prediction runs were used further in the study.

4.6 Accuracy of predicted and realised breeding performance

Pearson correlation coefficients (accuracy as described in section 3.7) between predicted breeding values from forward prediction runs ($\hat{g}_{fwd}$) and realised breeding performance values from backward prediction runs ($\hat{g}_{bwd}$) were estimated. Predicted breeding values in the F_1 trials were correlated to realised breeding performance in the F_2 trials and predicted breeding values in the F_2 trials were correlated to the realised breeding performance in the F_3 trials.

The accuracy (r_{fb}) between the F_1 BLUP breeding values and the F_2 BLUP breeding values are presented in Table 4.16 and those between the F_2 and F_3 BLUP breeding values are presented in Table 4.17 and Table 4.18. The accuracy for the single-trait

scenarios are given in Table 4.16, Table 4.17 and Table 4.18 as well. The significance of the correlations is indicated in the tables. Most of the correlations were significant for the correlations between the F_1 and F_2 data sets, except for a few of the partial pivoting Clipper and SVD with threshold of $1x10^{-1}$ correlations.

The accuracies (correlation coefficients) between the F_2 and F_3 trials were very low compared to those between the F_1 and F_2 trials and most were not significant at the 5% level of significance. There were a number of large $\hat{g}_{fwd}$ values (unstable cases) in the forward prediction runs of the F_2 trials which could have contributed towards the low correlations (Table 4.17 and Table 4.18). In order to assess the highest potential correlations that could be expected from this data set, the large $\hat{g}_{fwd}$ values were removed from the data set in SAS and the correlations were re-estimated (as described in section 3.7). This improved the magnitude of the accuracy, however the correlations remained non-significant at the 5% level of significance (Table 4.17 and Table 4.18). The relatively more stable F_1 *E. grandis* population data had fewer $\hat{g}_{fwd}$ outliers than the scenarios of the F_2 *E. grandis* population data. The mean accuracy over the ten economic weighting scenarios for the F_1F_2 and both the F_2F_3 sets of trials are given in Table 4.19 together with the single trait accuracies and compound heritabilities for further comparison.

The heritabilities of the compound weighted trait for the F_1 and F_2 trials are given in Table 4.16 to Table 4.19. The heritability of the compound weighted trait gives the benchmark against which the accuracy (correlations) of the different calculation methods was evaluated (as described in section 3.9). The evaluation was made using twice the accuracy ($2r_{fb}$) compared to the heritability of the compound weighted trait (as described in section 3.9).

Table 4.16 A comparison of the accuracy (r_{fb}) between the backward prediction $\hat{g}_{bwd}$ (F_2 *E. grandis* trials) and the forward prediction $\hat{g}_{fwd}$ (F_1 *E. grandis* trials) runs with the heritability of the compound weighted trait.

Economic weighting*	Method: Partial pivoting	Full pivoting	SVD[1]	SVD[2]	SVD[3]	Ridge regression	Low Partial pivoting	Low Full pivoting	2x Mean accuracy across method ($2r_{fb}$)	Heritability of compound weighted trait h_c^2
1	0.18085**	0.18085**	0.18085**	0.18094**	0.17594**	0.18158**	0.15204**	0.17513**	0.3507	0.310
2	0.21287***	0.21297***	0.21297***	0.21307***	0.21525***	0.21357***	0.18277***	0.20638***	0.4163	0.327
3	0.24601***	0.24607***	0.24607***	0.24603***	0.24448***	0.24719***	0.22406***	0.24038***	0.4841	0.349
4	0.26999***	0.27005***	0.27005***	0.26996***	0.26864***	0.27152***	0.25234***	0.26522***	0.5336	0.367
5	0.19056***	0.19071***	0.19071***	0.19860***	0.19860***	0.19084***	0.15526**	0.18428***	0.3740	0.309
6	0.10307*	0.10286*	0.10286*	0.10330*	0.08653ns	0.10429*	0.07928ns	0.09666*	0.1931	0.245
7	0.12816**	0.12810**	0.12810**	0.12833**	0.12020*	0.12907**	0.09652*	0.12480**	0.2443	0.275
8	0.19386***	0.19397***	0.19397***	0.19411***	0.19767***	0.19441***	0.16058**	0.18747***	0.3777	0.314
9	0.17519**	0.17535**	0.17535**	0.17549**	0.18468***	0.17540**	0.13795**	0.16937**	0.3410	0.296
10	0.10582*	0.10555*	0.10555*	0.10611*	0.08616ns	0.10689*	0.08747ns	0.10800*	0.2017	0.237
Single traits:										
DBH	0.18341***	0.18327***	0.18327***				0.17513**	0.17513**	0.360	0.292
Height	0.27487***	0.27487***	0.27487***				0.27699***	0.27699***	0.551	0.423
Stem form	0.19198***	0.19407***	0.19407***				0.19372***	0.19372***	0.387	0.207

Accuracy (correlation coefficient) significant effect: *** p<0.0001 ** p<0.01 * p<0.05 ns non-significant at p = 0.05

SVD[1] = SVD with threshold of $1x10^{-6}$; SVD[2] = SVD with threshold of $1x10^{-2}$; SVD[3] = SVD with threshold of $1x10^{-1}$

Low Partial pivoting is low precision in Clipper Matgen; Low Full pivoting is low precision in Clipper Matgen;

*For a description on the economic weighting sets please refer to Table 3.1.

Table 4.17 Accuracy (r_{fb}) between the backward prediction $\hat{g}_{bwd}$ (F_3 trials at Dukuduku) and the forward prediction $\hat{g}_{fwd}$ (F_2 trials) runs.

Economic weighting*	Method: Partial pivoting	Full pivoting	SVD ($1x10^{-6}$ threshold)	Ridge regression	Low Partial pivoting	Low Full pivoting	2x Mean accuracy across method ($2r_{fb}$)	Heritability of compound weighted trait h_c^2
1	-0.00459^{ns}	0.08518^{ns}	0.07600^{ns}	0.06404^{ns}	-0.01859^{ns}	0.07605^{ns}	0.04635	
	0.07573^{ns}	0.10442^{ns}	0.09490^{ns}	0.08142^{ns}	0.09533^{ns}	0.09494^{ns}	0.09112	0.285
2	0.04377^{ns}	0.08227^{ns}	0.07277^{ns}	0.05432^{ns}	-0.00554^{ns}	0.07275^{ns}	0.05339	
	0.08342^{ns}	0.09131^{ns}	0.08170^{ns}	0.06270^{ns}	0.09591^{ns}	0.08169^{ns}	0.08279	0.303
3	0.00397^{ns}	0.11558*	0.10556^{ns}	0.07766^{ns}	0.03721^{ns}	0.10555^{ns}	0.07426	
	0.07444^{ns}	0.12667*	0.11625^{ns}	0.08741^{ns}	0.10329^{ns}	0.11621^{ns}	0.10405	0.299
4	-0.00655^{ns}	0.12945*	0.11951*	0.08611^{ns}	0.02641^{ns}	0.11939*	0.07905	
	0.13358*	0.13411*	0.12364*	0.08921^{ns}	0.04257^{ns}	0.12355*	0.10778	0.303
5	0.02532^{ns}	0.05468^{ns}	0.04623^{ns}	0.03427^{ns}	0.02812^{ns}	0.04621^{ns}	0.03914	
	0.02333^{ns}	0.05807^{ns}	0.04940^{ns}	0.03755^{ns}	0.02383^{ns}	0.04940^{ns}	0.04026	0.312
6	-0.04047^{ns}	0.04193^{ns}	0.03858^{ns}	0.05895^{ns}	-0.04357^{ns}	0.03854^{ns}	0.01566	
	0.01574^{ns}	0.07649^{ns}	0.07296^{ns}	0.09009^{ns}	0.05104^{ns}	0.07293^{ns}	0.06321	0.257
7	-0.02048^{ns}	0.05449^{ns}	0.04751^{ns}	0.05134^{ns}	-0.02871^{ns}	0.04752^{ns}	0.02528	
	0.03631^{ns}	0.08283^{ns}	0.07556^{ns}	0.07724^{ns}	0.05939^{ns}	0.07556^{ns}	0.06782	0.275
8	0.01439^{ns}	0.06783^{ns}	0.05877^{ns}	0.04512^{ns}	0.00967^{ns}	0.05879^{ns}	0.04243	
	0.06792^{ns}	0.07885^{ns}	0.06955^{ns}	0.05542^{ns}	0.01125^{ns}	0.06955^{ns}	0.05876	0.303
9	0.00948^{ns}	0.04408^{ns}	0.03619^{ns}	0.02766^{ns}	0.01011^{ns}	0.03612^{ns}	0.02727	
	0.04823^{ns}	0.06202^{ns}	0.05377^{ns}	0.04450^{ns}	0.04285^{ns}	0.05370^{ns}	0.05085	0.312
10	-0.04923^{ns}	0.04185^{ns}	0.04020^{ns}	0.06709^{ns}	-0.05144^{ns}	0.04019^{ns}	0.01478	
	0.02244^{ns}	0.07935^{ns}	0.07759^{ns}	0.10087^{ns}	0.05622^{ns}	0.07757^{ns}	0.06901	0.248
Single traits:								
DBH	0.06517^{ns}	0.06642^{ns}	0.06517^{ns}		0.06523^{ns}	0.06642^{ns}	0.131	0.321
Height	0.19761**	0.19925**	0.19761**		0.19763**	0.19925**	0.397	0.322
Stem form	0.14423*	0.14423*	0.14423*		0.14425*	0.14423*	0.288	0.229

Accuracy (correlation coefficient) significant effect: *** p<0.0001 ** p<0.01 * p<0.05 ns non-significant at p = 0.05
Low Partial pivoting is low precision in Clipper Matgen; Low Full pivoting is low precision in Clipper Matgen;
First value for each method is before large breeding values were removed from the data sets. *For a description on the economic weighting sets please refer to Table 3.1.

Table 4.18 Accuracy (r_{fb}) between the backward prediction $\hat{g}_{bwd}$ (F_3 trials at Silverfontein) and the forward prediction $\hat{g}_{fwd}$ (F_2 trials) runs.

	Method							
Economic weighting*	**Partial pivoting**	**Full pivoting**	**SVD ($1x10^{-6}$ threshold)**	**Ridge regression**	**Low Partial pivoting**	**Low Full pivoting**	**2x Mean accuracy across method ($2r_{fb}$)**	**Heritability of compound weighted trait h_c^2**
1	-0.05137^{ns}	0.07966^{ns}	0.07151^{ns}	0.06813^{ns}	-0.03562^{ns}	0.07144^{ns}	0.03396	
	0.06818^{ns}	0.09424^{ns}	0.08587^{ns}	0.08320^{ns}	0.08441^{ns}	0.08578^{ns}	0.08361	0.285
2	0.09502^{ns}	0.09133^{ns}	0.08167^{ns}	0.06781^{ns}	-0.02749^{ns}	0.08162^{ns}	0.06499	
	0.08248^{ns}	0.09588^{ns}	0.08612^{ns}	0.07726^{ns}	0.05937^{ns}	0.08606^{ns}	0.08120	0.303
3	0.05910^{ns}	0.08756^{ns}	0.07749^{ns}	0.06310^{ns}	0.04186^{ns}	0.07752^{ns}	0.06777	
	0.10282^{ns}	0.10632^{ns}	0.09607^{ns}	0.08295^{ns}	0.02677^{ns}	0.09610^{ns}	0.08517	0.299
4	0.05324^{ns}	0.08978^{ns}	0.07933^{ns}	0.06168^{ns}	0.03303^{ns}	0.07924^{ns}	0.06605	
	0.11119^{ns}	0.11094^{ns}	0.10031^{ns}	0.08396^{ns}	0.00945^{ns}	0.10022^{ns}	0.08601	0.303
5	-0.01149^{ns}	0.09009^{ns}	0.08781^{ns}	0.08089^{ns}	0.01906^{ns}	0.08801^{ns}	0.05906	
	0.04172^{ns}	0.10607^{ns}	0.09678^{ns}	0.09053^{ns}	0.06182^{ns}	0.09698^{ns}	0.08232	0.312
6	-0.05837^{ns}	0.06387^{ns}	0.06167^{ns}	0.08482^{ns}	-0.05437^{ns}	0.06163^{ns}	0.02654	
	0.01729^{ns}	0.06885^{ns}	0.06653^{ns}	0.08738^{ns}	0.05892^{ns}	0.06650^{ns}	0.06091	0.257
7	-0.05652^{ns}	0.07488^{ns}	0.06917^{ns}	0.07820^{ns}	-0.04579^{ns}	0.06911^{ns}	0.03151	
	0.04327^{ns}	0.08524^{ns}	0.07930^{ns}	0.08765^{ns}	0.06735^{ns}	0.07925^{ns}	0.07368	0.275
8	-0.03638^{ns}	0.09194^{ns}	0.08274^{ns}	0.07552^{ns}	-0.01139^{ns}	0.08276^{ns}	0.04753	
	0.06466^{ns}	0.11035^{ns}	0.10099^{ns}	0.09425^{ns}	0.06365^{ns}	0.10102^{ns}	0.08915	0.303
9	-0.04185^{ns}	0.09752^{ns}	0.08891^{ns}	0.08488^{ns}	0.03958^{ns}	0.08889^{ns}	0.05966	
	0.10212^{ns}	0.11568^{ns}	0.10679^{ns}	0.10232^{ns}	0.02374^{ns}	0.10678^{ns}	0.09291	0.312
10	-0.05790^{ns}	0.05875^{ns}	0.05794^{ns}	0.08535^{ns}	-0.05679^{ns}	0.05323^{ns}	0.02343	
	0.00338^{ns}	0.06113^{ns}	0.06026^{ns}	0.08486^{ns}	0.07824^{ns}	0.06020^{ns}	0.05801	0.248
Single traits:								
DBH	0.18826^{**}	0.18826^{**}	0.19117^{**}		0.18829^{**}	0.19117^{**}	0.379	0.321
Height	0.08924^{ns}	0.09122^{ns}	0.08924^{ns}		0.08924^{ns}	0.09122^{ns}	0.180	0.322
Stem form	0.14823^{*}	0.14823^{*}	0.14823^{*}		0.14822^{*}	0.14823^{*}	0.296	0.229

Accuracy (correlation coefficient) significant effect: *** p<0.0001 ** p<0.01 * p<0.05 ns non-significant at p = 0.05
Low Partial pivoting is low precision in Clipper Matgen; Low Full pivoting is low precision in Clipper Matgen;
First value for each method is before large breeding values were removed from the data sets. *For a description on the economic weighting sets please refer to Table 3.1.

Table 4.19 Mean accuracy (over economic weight scenarios) and single trait accuracy ($2r_{fb}$) between the backward prediction ($\hat{g}_{bwd}$) and the forward prediction ($\hat{g}_{fwd}$) comparing collinearity mitigation techniques together with the mean compound heritability.

Scenarios	**Generations**	**Collinearity Mitigation Method used with BLUP**								**Mean heritability of compound weighted trait(h_c^2)**
		PP	**FP**	**SVD[3]**	**RR**	**Low PP**	**Low FP**	**SVD[1]**	**SVD[2]**	
Mean over 10 multiple-trait scenarios:	F_1F_2 *E. grandis*	0.36128	0.36128	0.36128	0.36296	0.30566	0.35154	0.36318	0.35564	0.303
	F_2F_3 *E. grandis*	-0.00488	0.14346	0.12826	0.11332	-0.00726	0.12822			0.290
Single traits:										
DBH	F_1F_2 *E. grandis*	0.36682^{***}	0.36654^{***}	0.36654^{***}		0.35026^{**}	0.35026^{**}			0.292
Height		0.54974^{***}	0.54974^{***}	0.54974^{***}		0.55398^{***}	0.55398^{***}			0.423
Stem form		0.38396^{***}	0.38814^{***}	0.38814^{***}		0.38744^{***}	0.38744^{***}			0.207
DBH	F_2F_3 *E. grandis*	0.13034^{ns}	0.13284^{ns}	0.13034^{ns}		0.13046^{ns}	0.13284^{ns}			0.321
Height		0.39522^{**}	0.39850^{**}	0.39522^{**}		0.39526^{**}	0.39850^{**}			0.322
Stem form		0.28846^{*}	0.28846^{*}	0.28846^{*}		0.28850^{*}	0.28846^{*}			0.229

Accuracy (correlation coefficient) significant effect: *** p<0.0001 ** p<0.01 * p<0.05 ns non significant

Significance not calculated for twice the mean r values among techniques over economic weighting scenarios

SVD = singular value decomposition; SVD^1 = SVD with threshold of $1x10^{-2}$; SVD^2 = SVD with threshold of $1x10^{-1}$; SVD^3 = SVD with threshold of $1x10^{-6}$ (standard threshold);

PP = partial pivoting control; FP = full pivoting; RR = ridge regression; Low = lower precision control in Clipper Matgen

Fisher's Least Significant Difference (LSD) multiple range tests ($\alpha = 0.05$) were run to assess whether significant differences existed between the mean accuracies, r_{fb}, (from Tables 4.16 to 4.18) of the different matrix inversion techniques and different numerical precision programmes for the F_1F_2 and the F_2F_3 scenarios. The results of these LSD multiple range tests are given in Table 4.20.

The LSD multiple range test between the mean r_{fb} for each matrix inversion technique, in each programme (Clipper Matgen and Delphi Matgen) in the F_1F_2 scenario, indicated a significant difference in the Clipper Matgen between the partial and full pivoting matrix inversion techniques, as indicated by the different letters in the LSD multiple range test (Table 4.20). There is also a significant difference between the full pivoting in low precision Clipper Matgen and all the high precision Delphi programme methods except for the SVD ($1x10^{-1}$) method. No significant difference in the F_1F_2 scenario was found between the mean r_{fb} of the full pivoting, partial pivoting, SVD ($1x10^{-2}$) matrix inversion methods and ridge regression in the Delphi Matgen programme for this set of trial data (Table 4.20).

In the F_2F_3 scenario with the Dukuduku F_3 trials (before the large $\hat{g}_{fwd}$ values were removed from the data set) the LSD multiple range test between the mean r_{fb} for each matrix inversion technique, in each programme (Clipper Matgen and Delphi Matgen), indicated that there was a significant difference between the partial pivoting method and the rest of the techniques in the Delphi programme (Table 4.20). In the Clipper Matgen programme the LSD multiple range test indicated that there was a significant difference between the partial pivoting and the full pivoting methods for this set of trial data (Table 4.20). There were no significant differences between the mean r_{fb} of the full pivoting, SVD matrix inversion methods and ridge regression in the Delphi programme for this set of trial data (Table 4.20). The partial pivoting methods of both programmes, although not significantly different from each other, differed significantly from the full pivoting, SVD matrix inversion, ridge regression and full pivoting Clipper methods (Table 4.20). When the large $\hat{g}_{fwd}$ values were removed from the data, the partial pivoting (both Clipper and Delphi methods) were significantly different from the full pivoting methods (both Clipper and Delphi methods) and the SVD Delphi programme method (Table 4.20).

In the F_2F_3 scenario with the Silverfontein F_3 trials (before the large $\hat{g}_{fwd}$ values were removed from the data set) the LSD multiple range test between the mean r_{fb} for each matrix inversion technique, in each programme (Clipper Matgen and Delphi Matgen), indicated that there was a significant difference between the partial pivoting method (both Clipper and Delphi methods) and the rest of the techniques in the Delphi programme and the full pivoting method of the Clipper Matgen programme. There were no significant differences between the mean r_{fb} of the full pivoting, ridge regression and SVD matrix inversion methods in the Delphi programme for this set of trial data (Table 4.20). In the Clipper Matgen programme the LSD multiple range test indicated a significant difference between the partial pivoting and the full pivoting methods for this set of trial data (Table 4.20). The partial pivoting methods of both programmes, although not significantly different from each other, differed significantly from the full pivoting, SVD matrix inversion, ridge regression and full pivoting Clipper methods (Table 4.20). When the large $\hat{g}_{fwd}$ values were removed from the data set the significant differences between the methods remained the same as when the large $\hat{g}_{fwd}$ values were included in the data set. The data from the F_2F_3 scenarios was still used further in the study as the accuracy (correlations between predicted and realised performance) is just one possible association or indicator for testing the efficiency of selection over generations and does not mean that the data in the forward selection runs was invalid or unreliable.

Table 4.20 Fisher's Least Significant Difference multiple range test for the mean accuracy (mean r_{fb}) of the F_1F_2 scenario and F_2F_3 scenarios (means with the same letter are not significantly different from each other at $\alpha = 0.05$).

Scenario	Method	n	LSD	Mean r_{fb}
F_1F_2	SVD($1x10^{-2}$ threshold)	10	A	0.18159
	Ridge	10	A	0.18148
	Full pivoting	10	A	0.18065
	Partial pivoting	10	A	0.18064
	SVD($1x10^{-1}$ threshold)	10	AB	0.17782
	Full pivoting Clipper	10	B	0.17577
	Partial pivoting Clipper	10	C	0.15301
F_2F_3 Dukuduku (Before large $\hat{g}_{fwd}$ removed)	Full pivoting	10	A	0.07173
	SVD ($1x10^{-6}$ threshold)	10	A	0.06413
	Full pivoting Clipper	10	A	0.06411
	Ridge	10	A	0.05666
	Partial pivoting	10	B	-0.00244
	Partial pivoting Clipper	10	B	-0.00363
F_2F_3 Dukuduku (Large $\hat{g}_{fwd}$ removed)	Full pivoting	10	A	0.08941
	SVD ($1x10^{-6}$ threshold)	10	AB	0.08153
	Full pivoting Clipper	10	AB	0.08151
	Ridge	10	BC	0.07264
	Partial pivoting Clipper	10	C	0.05817
	Partial pivoting	10	C	0.05811
F_2F_3 Silverfontein (Before large $\hat{g}_{fwd}$ removed)	Full pivoting	10	A	0.08083
	Ridge	10	A	0.07531
	SVD ($1x10^{-6}$ threshold)	10	A	0.07447
	Full pivoting Clipper	10	A	0.07398
	Partial pivoting	10	B	-0.01267
	Partial pivoting Clipper	10	B	-0.01323
F_2F_3 Silverfontein (Large $\hat{g}_{fwd}$ removed)	Full pivoting	10	A	0.09847
	SVD ($1x10^{-6}$ threshold)	10	A	0.08790
	Full pivoting Clipper	10	A	0.08789
	Ridge	10	A	0.08744
	Partial pivoting	10	B	0.06371
	Partial pivoting Clipper	10	B	0.05337

A further comparison was made between the mean correlations across the techniques and the compound heritabilities for each economic weighting set for each population scenario (see Figures 4.5 and 4.6). In Figure 4.5 the F_1F_2 *E. grandis* population data illustrates that twice the correlation coefficient value ($2r_{fb}$) against the compound

heritability value (h_c^2) is approximately the expected relationship, further indicating greater stability in this case than in the F_2F_3 case (refer to section 3.9 for an explanation for the use of this method of comparison). The F_2F_3 *E. grandis* data showed a substantial under performance of the $2r_{fb}$ value relative to the compound heritability value, h_c^2 (Figure 4.6 and Figure 4.7).

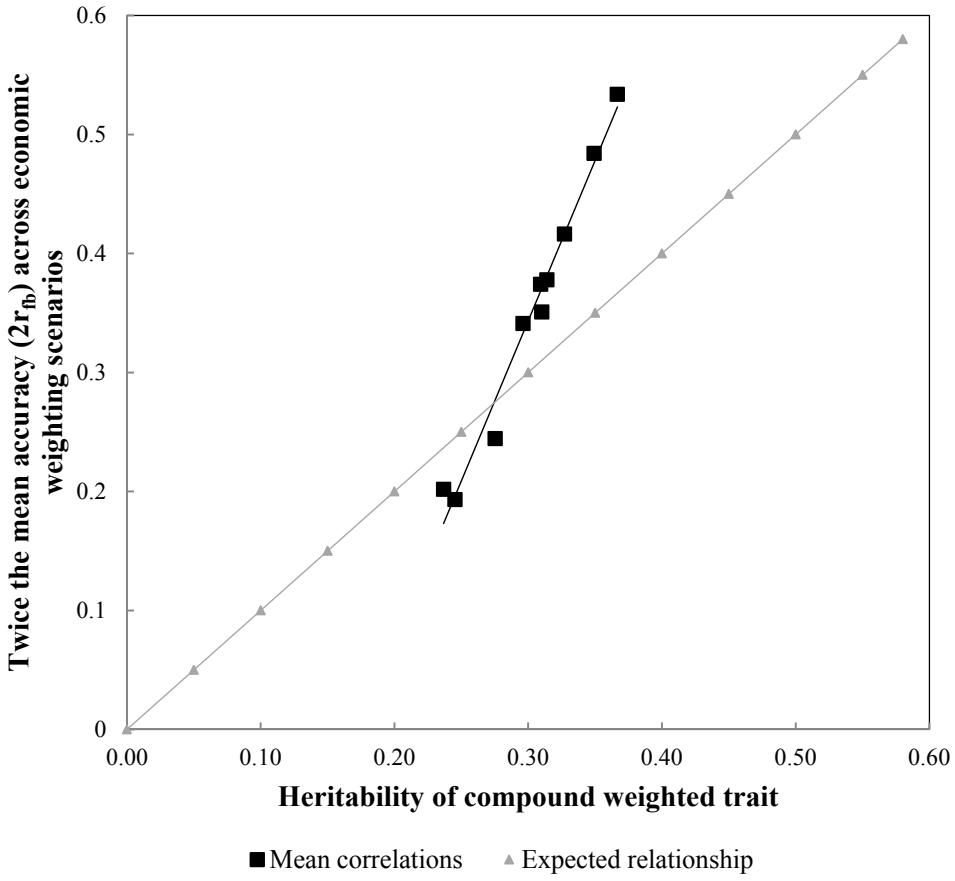

Figure 4.5 Twice the mean correlations ($2r_{fb}$) across the economic weighting scenarios relative to the heritability of the compound weighted trait across the same economic weighting scenarios for the F_1F_2 *E. grandis* population data. The diagonal line represents the expected linear relationship between the correlations and the heritability of the compound weighted trait.

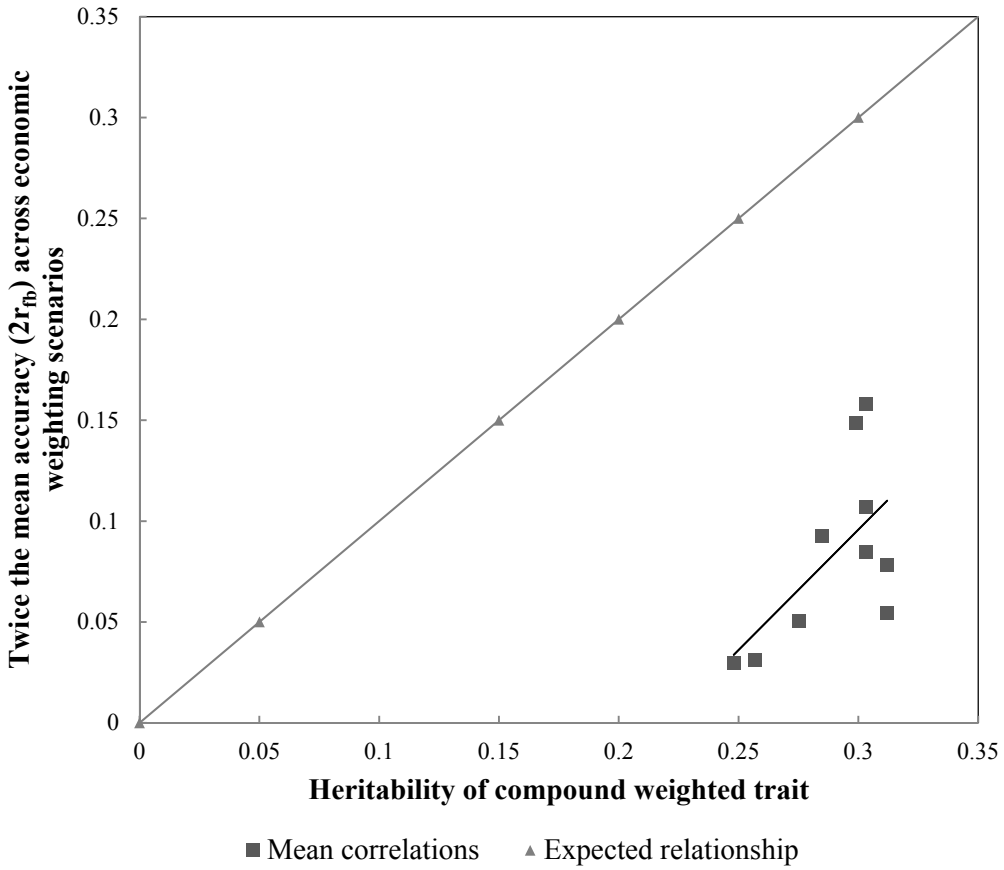

Figure 4.6 Twice the mean correlations ($2r_{fb}$) across the economic weighting scenarios relative to the heritability of the compound weighted trait across the same economic weighting scenarios for the F_2F_3 *E. grandis* population data at the Dukuduku plantation. The diagonal line represents the expected linear relationship between the correlations and the heritability of the compound weighted trait.

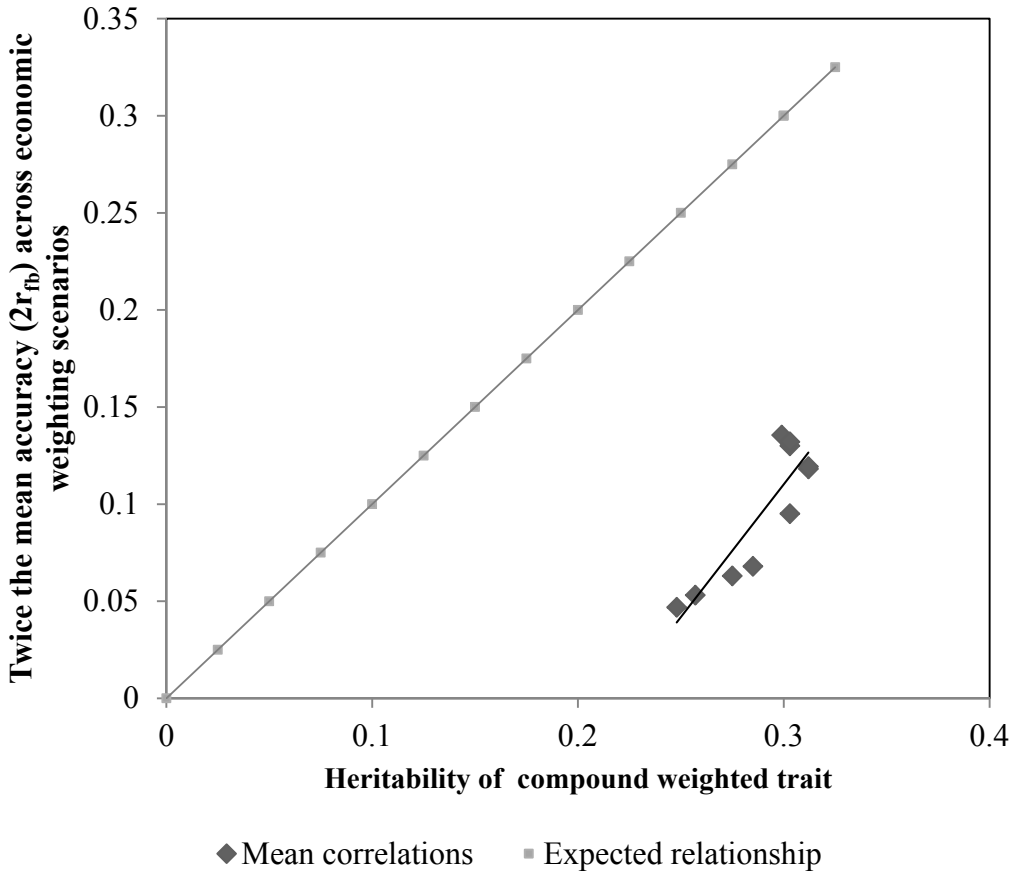

Figure 4.7 Twice the mean correlations ($2r_{fb}$) across the economic weighting scenarios relative to the heritability of the compound weighted trait across the same economic weighting scenarios for the F_2F_3 *E. grandis* population data at the Silverfontein plantation. The diagonal line represents the expected linear relationship between the correlations and the heritability of the compound weighted trait.

4.7 Rank correlation comparisons

Rank correlations were calculated for the forward prediction runs of the F_1 and F_2 trials to assess whether there were any significant BLUP index rank changes in the ranking of individuals in the forward predictions between the higher and lower precision programmes. Spearman rank correlation coefficients were calculated in SAS (the full table of these rank correlations can be found in Appendix A Table A8).

Small rank changes between the matrix inversion techniques when comparing the Clipper programmes with each other were observed in the F_1 trials and the rank correlations ranged from r = 0.974 to r = 0.994 over the different economic weightings. In the Delphi Matgen programme there were very few significant rank changes between SVD, full-pivoting Gaussian elimination and partial-pivoting Gaussian elimination matrix inversion techniques in the F_1 trials with correlations nearing one. There were some changes in ranks in the Delphi Matgen programme between the different matrix inversion techniques and ridge regression (r = 0.994 to r = 0.998 over the economic weight cases). Some rank changes were also present between the Clipper and Delphi programmes in the F_1 trials where correlations ranged from 0.932 to 0.952 for the different matrix inversion techniques and ranged from 0.923 to 0.948 between the Clipper matrix inversion techniques and ridge regression. In the case of the single-trait scenarios the correlation coefficients for the ranks were equal to one or close to one for the different methods in the Delphi programme for all three traits and also equal to one for the two Clipper programmes with each other. Very few rank differences were observed between Delphi and Clipper for the single-trait scenarios with correlation coefficients of r = 0.94 observed. All the rank correlations for the F_1 trials were significant at $p < 0.0001$.

Large rank differences were observed between the two Clipper programmes in the F_2 trials and rank correlation coefficients ranged from r = 0.816 to 1.000 over the different economic weightings for the F_2 data sets. Few rank changes were observed between the SVD and Gaussian full pivoting techniques in the Delphi Matgen programme with correlations close to one (r > 0.99). Some rank changes were present between the partial pivoting technique (PP) and the full pivoting (FP), SVD and ridge techniques in the Delphi programme where correlations ranged between 0.937 to 0.962 (PP and SVD), 0.936 to 0.962 (PP and FP) and 0.897 to 0.938 (PP and ridge). Some rank changes were also present between SVD and Gaussian full pivoting with ridge regression where correlation coefficients ranged between 0.959 and 0.988. In the single-trait scenarios the correlation coefficients for the ranks were equal to one for the Delphi Matgen techniques.

A range of 0.897 to 0.944 correlation in ranks was observed between the two Clipper methods and between the Delphi Matgen and Clipper Matgen methods with each other. All rank correlations for the F_2 trials were significant at $p < 0.0001$.

4.8 Realised genetic gains

The realised genetic gains, expressed in terms of standard deviation units, were calculated for each economic weighting set and each of the matrix inversion methods (Delphi and Clipper) and ridge regression runs. The mean of the predicted breeding values of the backward prediction runs of the F_2 and the F_3 trials were used in calculating the realised gains (Ruotsalainen & Lindgren 1998; Silva *et al*. 2000) for the top five and bottom five percent of the forward prediction families in the F_1 and F_2 trials respectively as described in the methods section 3.7.

The variance of the genetic gains (in standard deviation units) among mitigation techniques within scenarios is shown in Table 4.21.

Table 4.21 The variance of realised genetic gains (in standard deviation units) between techniques within scenarios in the *E. grandis* population data.

Species & plantation	**Selection Population**	**Performance measured in**	**Variance of genetic gains***	
			Top %	**Bottom %**
E. grandis	F_1	F_2	0.0016	0.0014
E. grandis Dukuduku	F_2	F_3	0.0028	0.0032
E. grandis Silverfontein	F_2	F_3	0.0006	0.0073

* Eucalypts top and bottom percentage is 5%

The realised gains for the F_1F_2 *E. grandis* scenario and those for the F_2F_3 *E. grandis* scenarios are presented in Table A9 - Table A11 in Appendix A.

In the F_1F_2 scenarios and the two F_2F_3 scenarios the improvement in realised genetic gains varied in magnitude over the different economic weighting sets (see Table 3.1 for the economic weightings used) and differences in gains were also found between the different matrix inversion methods (see Tables A9 to A11 in Appendix A).

In the F_1F_2 *E. grandis* scenarios both the high numerical precision and the lower numerical precision programmes gave similar mean realised gains for all the different techniques used, however the partial pivoting Clipper method had significantly (at $\alpha = 0.05$) less gains than the other techniques (Table A9). In the F_2F_3 *E. grandis* scenarios significant differences (at $\alpha = 0.05$) in realised genetic gains occurred between the partial pivoting techniques (both programmes) and the rest of the techniques used across the programmes (Table A10 and Table A11).

In the F_1F_2 scenario, the largest difference in the realised genetic gains of the top five percent of families, between the technique having the lowest gains and the best alternative technique, was a 100 % improvement or difference of 0.05 standard deviation units (economic weighting set nine – see Table 3.1 for description of weighting) and is illustrated in Figure 4.8 below. In the bottom five percent of families the largest difference in realised genetic gains was an improvement of 115.6 % (economic weighting set seven – see Table 3.1 for description of weighting) or a difference of 0.06 standard deviation units and is illustrated in Figure 4.9 below. In all but one case (where it was equal to) the partial pivoting Clipper technique had lower gains compared to the best alternative technique. In the top five percent of families the range in realised genetic gains among techniques within economic weighting scenarios ranged from a difference of 0.01 to 0.05 in standard deviation units between techniques and in the bottom five percent of families from a difference of 0.01 to 0.06 in standard deviation units between techniques (Table A9 in Appendix A).

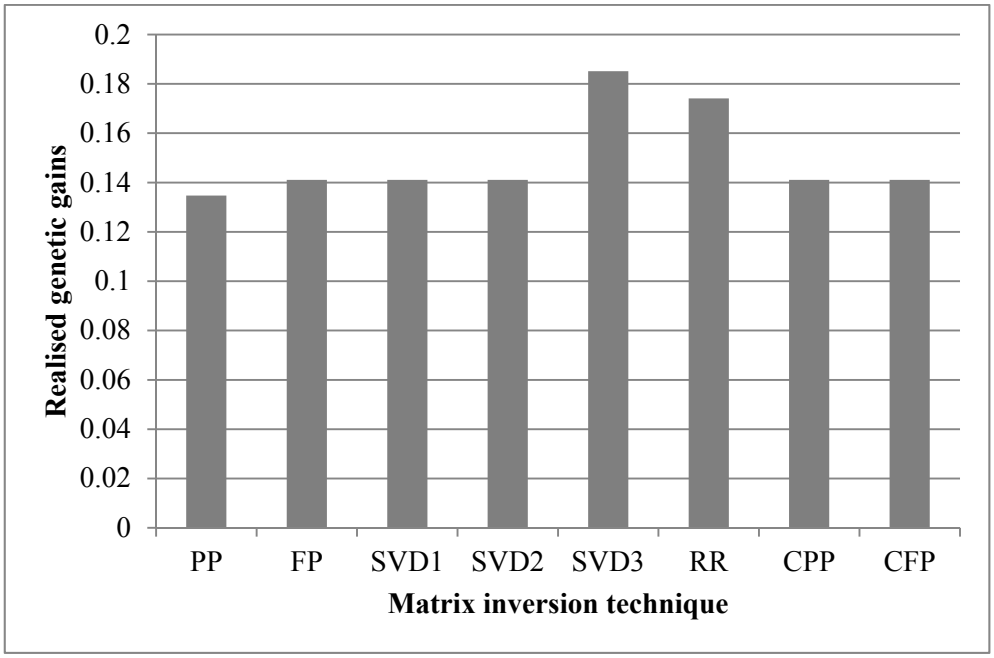

Figure 4.8 Realised genetic gains (standard deviation units) in the F_2 *E. grandis* population data for economic weighting scenario nine from the top 5% of F_1 breeding value selections. Techniques in higher precision Delphi: partial pivoting (PP), full pivoting (FP), singular value decomposition (SVD1 = SVD with threshold of $1x10^{-6}$; SVD2 = SVD with threshold of $1x10^{-2}$; SVD3 = SVD with threshold of $1x10^{-1}$), ridge regression (RR) and in lower precision Clipper: partial pivoting (CPP) and full pivoting (CFP).

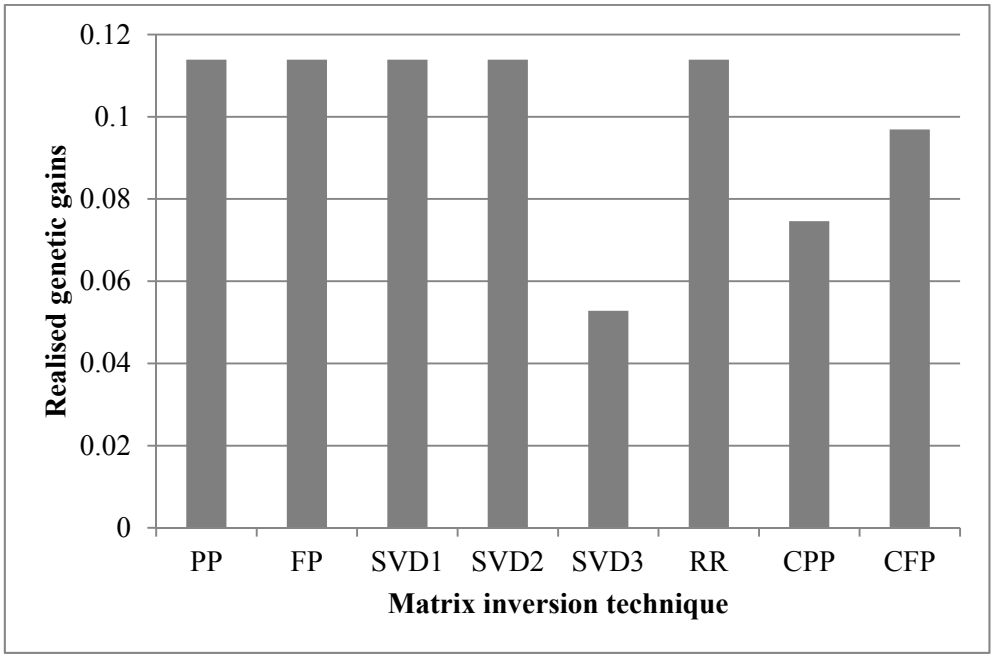

Figure 4.9 Realised genetic gains (standard deviation units) in the F_2 *E. grandis* population data for economic weighting scenario seven from the bottom 5% of F_1 breeding value selections. Techniques in higher precision Delphi: partial pivoting (PP), full pivoting (FP), singular value decomposition (SVD1 = SVD with threshold of $1x10^{-6}$; SVD2 = SVD with threshold of $1x10^{-2}$; SVD3 = SVD with threshold of $1x10^{-1}$), ridge regression (RR) and in lower precision Clipper: partial pivoting (CPP) and full pivoting (CFP). The negative signs for the bottom 5% gains have been reversed for this plot.

The realised genetic gains in the F_2F_3 scenario at Dukuduku also varied in magnitude over the different economic weightings. In the F_2F_3 scenario at Dukuduku (Table A10 in Appendix A), the largest difference in the realised genetic gains of the top five percent of families, between the technique having the lowest gains and the best alternative technique within the same economic weighting scenario (see Table 3.1 for a description of economic weightings), was 324 times more improvement or a 0.143 difference in standard deviation units (economic weighting set eight). This large improvement does, however, depend on the very low gains in the partial pivoting technique in this economic weighting scenario. The largest difference in the realised genetic gains in the bottom five percent of families (Table A10 in Appendix A) was a 246 times more

improvement or a difference of 0.215 standard deviation units (economic weighting set ten – see Table 3.1 for description of economic weightings). Figures 4.10 and 4.11 illustrate the above differences. In all economic weighting cases the partial pivoting Clipper technique had lower gains than the best alternative technique. The range in the realised gains in the top five percent of families among techniques within economic weighting scenarios ranged from a difference of 0.04 to 0.14 in standard deviation units between techniques (Table A10 in Appendix A). In the bottom five percent of families the range in realised genetic gains ranged from a difference of 0.03 to 0.22 in standard deviation units between techniques (Table A10 in Appendix A).

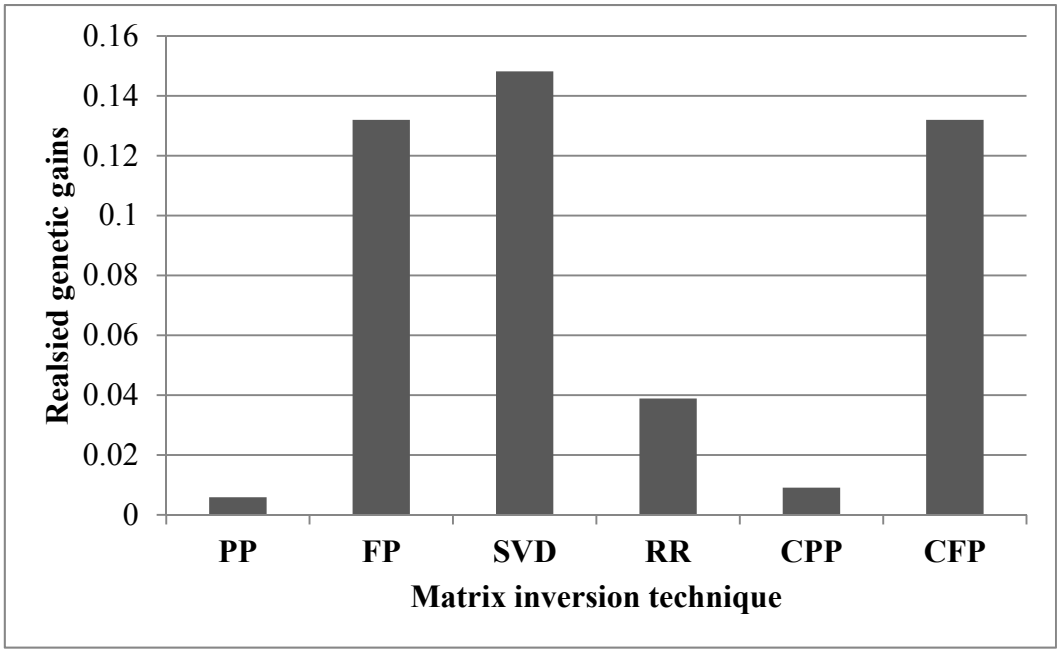

Figure 4.10 Realised genetic gains (standard deviation units) in the F_3 *E. grandis* population data at Dukuduku for economic weighting scenario eight from the top 5% of F_2 breeding value selections. Techniques in higher precision Delphi: partial pivoting (PP), full pivoting (FP), singular value decomposition (SVD), ridge regression (RR) and in lower precision Clipper: partial pivoting (CPP) and full pivoting (CFP).

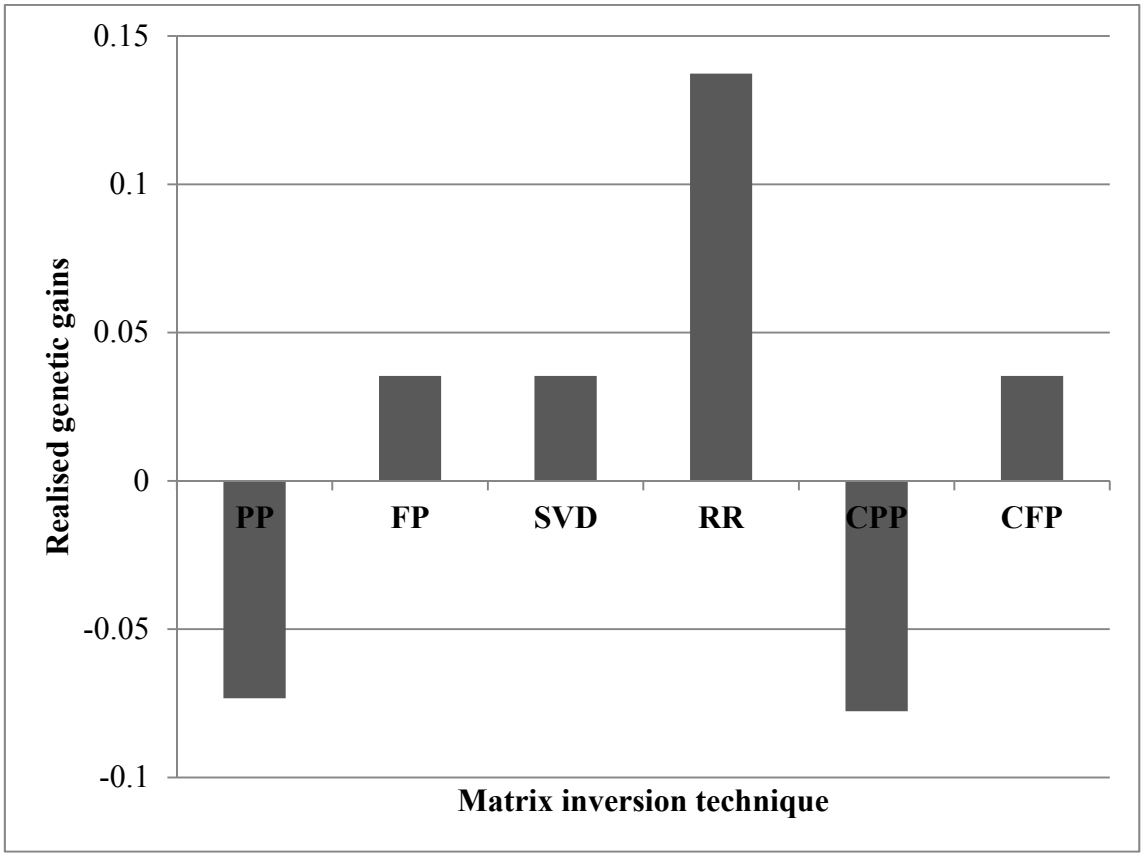

Figure 4.11 Realised genetic gains (standard deviation units) in the F_3 *E. grandis* population data at Dukuduku for economic weighting scenario ten from the bottom 5% of F_2 breeding value selections. Techniques in higher precision Delphi: partial pivoting (PP), full pivoting (FP), singular value decomposition (SVD), ridge regression (RR) and in lower precision Clipper: partial pivoting (CPP) and full pivoting (CFP). The signs for the gain values have been reversed in this Figure for easier comparison to the top gains Figure.

The realised genetic gains varied in magnitude over the different economic weightings in the F_2F_3 scenario at Silverfontein. In the F_2F_3 scenario at Silverfontein, the largest difference in the realised genetic gains of the top and bottom five percent of families, between the technique having the lowest gains and the best alternative technique, was a 110 % improvement or a difference of 0.07 standard deviation units (economic weighting set five) and a 164 % improvement in gains or difference of 0.28 standard deviation units (economic weighting set seven) respectively (see Table A11 in Appendix A). These differences are illustrated in Figures 4.12 and 4.13 below. In all

economic weighting cases the partial pivoting Clipper technique had lower gains than the best alternative technique. In the top five percent of families the improvement in realised genetic gains ranged from a difference of 0.02 to 0.07 in standard deviation units between techniques (Table A11 in Appendix A). The improvement in realised genetic gains in the bottom five percent of families ranged from a difference of 0.03 to 0.28 in standard deviation units between techniques (Table A11 in Appendix A).

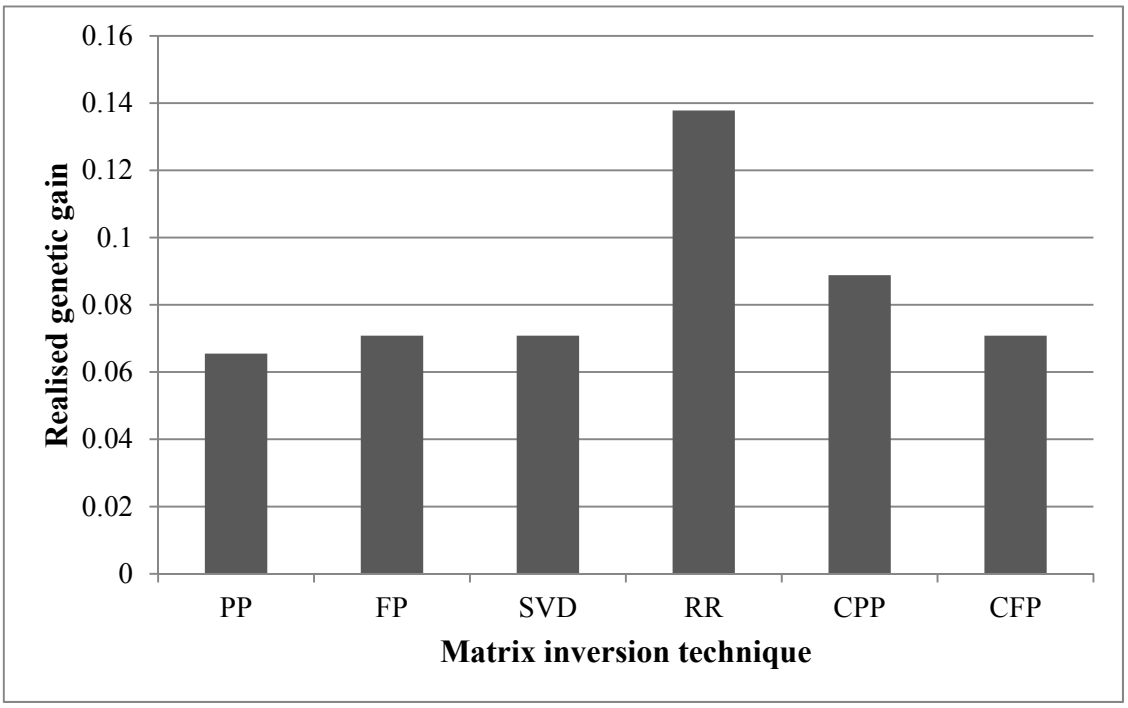

Figure 4.12 Realised genetic gains in the F_3 *E. grandis* population data at Silverfontein for economic weighting scenario five from the top 5% of F_2 breeding value selections. Techniques in higher precision Delphi: partial pivoting (PP), full pivoting (FP), singular value decomposition (SVD), ridge regression (RR) and in lower precision Clipper: partial pivoting (CPP) and full pivoting (CFP).

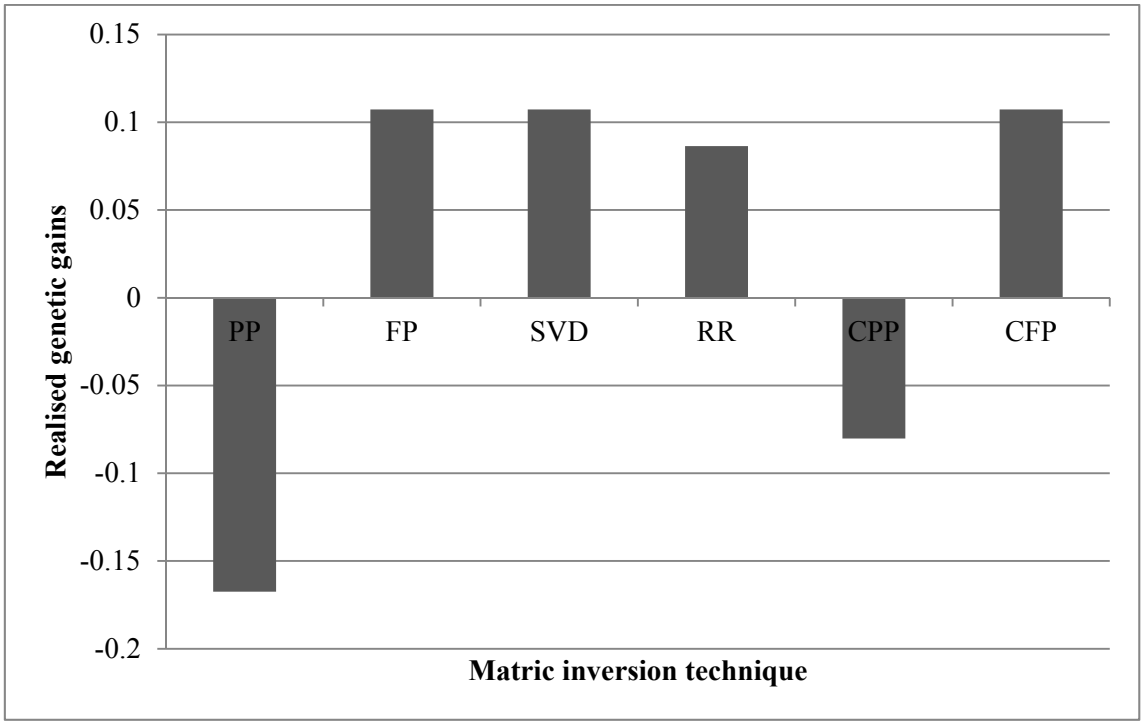

Figure 4.13 Realised genetic gains in the F_3 *E. grandis* population data at Silverfontein for economic weighting scenario seven from the bottom 5% of F_2 breeding value selections. Techniques in higher precision Delphi: partial pivoting (PP), full pivoting (FP), Singular Value D Decomposition (SVD), ridge regression (RR) and in lower precision Clipper partial pivoting (CPP) and full pivoting (CFP). The signs for the gains values have been reversed in this Figure for easier comparison with the top gains Figure.

An analysis of variance (using Proc GLM in SAS) and LSD multiple range test was executed in SAS on the gains data (combination of both the top and bottom 5 % gains values) for the F_1F_2 and F_2F_3 *E. grandis* scenarios. The economic weights effect was highly significant ($p < 0.0001$) for the F_1F_2 scenario and the F_2F_3 scenario ($p < 0.0001$) at Silverfontein and was not significant for the F_2F_3 scenario at Dukuduku. The techniques effect (the different matrix inversions and ridge regression) was highly significant for the F_2F_3 scenarios at Dukuduku and Silverfontein ($p < 0.0001$) but was not significant for the F_1F_2 scenario at the 95 % level of confidence. At the 90% level of confidence the techniques effect of the F_1F_2 scenario would however have been significant. The results of the LSD multiple range tests are given in Table 4.22 below.

Table 4.22 Fisher's Least Significant Difference multiple range test for the mean of the top 10% and bottom 10% realised genetic gains in standard deviation units over the economic weightings for the F_1F_2 and F_2F_3 *E. grandis* scenarios (means with the same letter are not significantly different from each other at $\alpha = 0.05$).

Scenario	**Method**	**n**	**LSD**	**Mean Gains**
F_1F_2	Ridge	20	A	0.12107
	SVD($1x10^{-2}$ threshold)	20	A	0.11795
	Full pivoting	20	A	0.11768
	Full pivoting Clipper	20	A	0.11756
	Partial pivoting	20	A	0.11710
	SVD($1x10^{-1}$ threshold)	20	A	0.11316
	Partial pivoting Clipper	20	B	0.10066
F_2F_3 Dukuduku	Full pivoting	20	A	0.08849
	SVD ($1x10^{-6}$ threshold)	20	A	0.08543
	Full pivoting Clipper	20	A	0.08514
	Ridge	20	A	0.06474
	Partial pivoting	20	B	0.01892
	Partial pivoting Clipper	20	B	0.00765
F_2F_3 Silverfontein	Ridge	20	A	0.09083
	Full pivoting	20	A	0.08605
	Full pivoting Clipper	20	A	0.08294
	SVD ($1x10^{-6}$ threshold)	20	A	0.08239
	Partial pivoting Clipper	20	B	0.03859
	Partial pivoting	20	B	0.03244

CHAPTER 5
RESULTS: *PINUS PATULA* TRIALS

5.1 Introduction

In the CSIR pine breeding programme, the most suitable data was found in the *P. patula* part of the pine programme where there were trials available with data from two generations of breeding. Fourteen F_1 and six F_2 trials with suitably aged data and traits were available to investigate the remediation of potential instability in Best Linear Unbiased Prediction (BLUP) in tree breeding population data. Genetic parameters were estimated for these trials and the predicted breeding values and realised breeding performance were estimated using different matrix inversion techniques and an adapted ridge regression (only for predicted breeding value) within BLUP. The predicted breeding values and realised breeding performances were correlated to estimate the accuracy and the use of different computational methods and different matrix inversion techniques were compared. The results from these *P. patula* trials are presented in this chapter.

5.2 Data Editing

The data from the above trials were explored and edited using SAS before any further analysis was performed. Tests for the normality of residuals and for the significance of effects were also run on all the trial data prior to analysis. The trees for which no height or diameter at breast height (DBH) values were available (dead or missing trees) and outliers (observations that were far from the mean i.e. trees with much larger or smaller DBH, heights and stem form values than the trial mean as described in section 3.3) were deleted from the data set before further analysis was carried out.

5.2.1 Tests for Normality

Tests for normality of the residuals were run for each data set prior to the removal of missing data and outliers. These tests of normality included the Shapiro-Wilk statistic, skewness, kurtosis and normal probability tests.

As explained in Chapter 4, the Shapiro-Wilk statistic (W) test's null hypothesis is that the residuals are normally distributed. In the *P. patula* data sets some of the trials had sample sizes larger than 2000 and for these trials the Kolmogorov-Smirnov statistic (D) test was used. As in the Shapiro-Wilk test values of p that are greater than 0.05 will lead to the acceptance of the null hypothesis of normally distributed residuals at the 5% level of significance. The Shapiro-Wilk and Kolmogorov-Smirnov test p values for the *P. patula* trials are presented in Table 5.1.

In all of the *P. patula* F_1 trials the residuals for height and stem form were not normally distributed according to the Shapiro-Wilk and Kolmogorov-Smirnov tests. In the *P. patula* F_1 trials for the DBH variable, only trials 1010303PF4002.02 (Tweefontein), 1010803PF4003, 1010802PF4004, 1010803PF4005.01 and 02 and 1010803PF4006.01 (Tweefontein) had residuals that were normally distributed. In all of the F_2 trials for the stem form and height variables the residuals were not normally distributed. The residuals for DBH were normally distributed only in F_2 trials 1010803PF4015 (at Tweefontein and Wilgeboom) and trial 1010803PF4011.02 (at Mac Mac).

Skewness and kurtosis were further measures used to assess the normality of the residuals in the *P. patula* trials (for an explanation on these measures see Chapter 4 section 4.2.1). The skewness and kurtosis values for the *P. patula* trials are presented in Table 5.1. In the F_1 trials most of the trials had negative skewness values for DBH and height and positive skewness values for stem form. In the F_2 trials most had negative values for skewness for DBH and height. Half of the values for skewness for stem form were negative and the other half positive. The kurtosis values were positive for the height trait in the F_1 trials. Some of these trials had large positive kurtosis values that indicated leptokurtic distribution of data in those trials. The kurtosis values were positive for the DBH trait in most cases, but trials 1010803PF4005 (Tweefontein and

Wilgeboom) and 1010803PF4006.02 (Jessievale) had negative kurtosis values. For the height trait three trials had negative kurtosis values (1010803PF4002.01 Belfast, 1010803PF4007.01 Jessievale and 1010803PF4010 Jessievale). In the F_2 trials there were more trials with small negative kurtosis than positive kurtosis for DBH, height and stem form traits indicating platykurtic distribution of data in those trials.

Normal probability plots of the residuals were a further measure of normality considered for the *P. patula* trials. The normal probability plots are shown in Figures 5.1 and 5.2. In all of the F_1 and F_2 trials there were some deviations from normality in all three selection traits. Following removal of missing values and the outliers from the data sets an improvement in the normality of the distributions (skewness and kurtosis values closer to zero) was observed. All data was corrected for fixed effects and also standardized which normalises the variables (as mentioned in Chapter 3 section 3.3). Where possible, as with the *E. grandis* data, methods that were more suited to data which is unbalanced and not completely normally distributed (such as the generalised least squares methods (GLM) and restricted maximum likelihood (REML) methods) were used in subsequent analyses. BLUP can handle data which is not completely normally distributed and deviations from normality do not decrease the accuracy of the estimated breeding values derived from BLUP (Goddard 1992).

Table 5.1 Normality of residuals test statistics for the F_1 and F_2 *P. patula* trials.

	Measures of the normality of distribution of residuals for selection traits			
Trial	**Trait**	**Shapiro-Wilk or Kolmogorov-Smirnov* Pr < W or Pr > D**	**Skewness**	**Kurtosis**
1010303PF4002.01 Belfast	DBH	<0.0001	-0.4507	0.4404
	Height	<0.0001	-0.5891	0.9663
	Stem	0.0115	0.1729	-0.0056
1010303PF4002.02 Tweefontein	DBH	0.8474	0.1654	0.1010
	Height	0.0003	-0.4990	1.7186
	Stem	0.0017	0.3568	0.8585
1010803PF4003 Rietfontein	DBH	0.1183	0.1253	0.2143
	Height	<0.0001	-1.2068	1.5408
	Stem	<0.0001	-0.1441	0.4747
1010803PF4004 Wilgeboom	DBH	0.3406	0.0402	0.0318
	Height	<0.0001	-0.6820	1.8436
	Stem	<0.0001	-0.4496	0.4388
1010803PF4005.01 Wilgeboom	DBH	0.0795	0.0780	-0.2097
	Height	<0.0001	-0.3713	0.2190

Trial	Measures of the normality of distribution of residuals for selection traits			
	Trait	**Shapiro-Wilk or Kolmogorov-Smirnov* Pr < W or Pr > D**	**Skewness**	**Kurtosis**
	Stem	<0.0001	-0.4502	0.4011
1010803PF4005.02 Tweefontein	DBH	0.5479	0.0626	-0.0272
	Height	<0.0001	0.5179	2.0857
	Stem	<0.0001	-0.7934	1.0292
1010803PF4006.01 Tweefontein	DBH	>0.1500*	-0.0191	0.4335
	Height	<0.0100*	-0.2695	0.9642
	Stem	<0.0100*	0.5722	0.1519
1010803PF4006.02 Jessievale	DBH	0.0342	-0.1605	-0.0334
	Height	<0.0001	-0.3090	0.4902
	Stem	<0.0001	-0.2579	0.2872
1010803PF4007.01 Jessievale	DBH	0.0092	-0.1991	0.0969
	Height	<0.0001	1.1932	19.6516
	Stem	0.0083	0.0527	-0.0401
1010803PF4007.02 Frankfort	DBH	<0.0001	-0.6837	1.4356
	Height	<0.0001	-0.2295	0.8878
	Stem	0.0002	0.4097	0.8037
1010803PF4008.01 Tweefontein	DBH	<0.0100*	-0.3644	0.3860
	Height	<0.0100*	-0.7324	1.3246
	Stem	<0.0100*	0.0113	1.6201
1010803PF4008.02 Jessievale	DBH	<0.0001	-0.2857	0.5270
	Height	<0.0001	-0.6024	1.3741
	Stem	<0.0001	0.8082	1.0754
1010803PF4009 Jessievale	DBH	<0.0100*	-0.2257	0.0853
	Height	<0.0100*	-0.5557	1.0517
	Stem	<0.0100*	-0.0314	0.0448
1010803PF4010 Jessievale	DBH	<0.0100*	-0.5383	0.8663
	Height	<0.0100*	-0.9787	2.4466
	Stem	<0.0100*	0.1633	-0.3534
1010803PF4011.01 Wilgeboom	DBH	0.0394	0.0890	-0.3021
	Height	<0.0001	-0.3427	-0.3233
	Stem	<0.0001	0.2511	-0.0886
1010803PF4011.02 Mac-Mac	DBH	0.1086	-0.1371	0.0202
	Height	<0.0001	-0.3505	-0.0513
	Stem	<0.0001	-0.1114	-0.4905
1010803PF4011.03 Tweefontein	DBH	<0.0001	-0.2696	0.0373
	Height	<0.0001	-0.4462	-0.0344
	Stem	<0.0001	0.2463	0.5409
1010803PF4011.04 Frankfort	DBH	0.0126	-0.2244	-0.0463
	Height	<0.0001	-0.4657	0.1139
	Stem	0.0005	0.2839	0.0386
1010803PF4015.01 Tweefontein	DBH	0.0836	-0.2766	0.4947
	Height	<0.0001	-0.7389	1.6176
	Stem	<0.0001	-0.4520	-0.2159
1010803PF4015.02 Wilgeboom	DBH	0.5635	-0.0913	0.0164
	Height	<0.0001	-1.0155	3.7565
	Stem	<0.0001	-0.6018	-0.0824

W refers to the Shapiro Wilk test statistic value
D refers to the Kolmogorov-Smirnov test statistic value
Pr < W or Pr > D refers to the p value of the probability of obtaining the test statistic W or D

Figure 5.1 Normal probability plots for each selection trait in the F_1 *P. patula* trials.

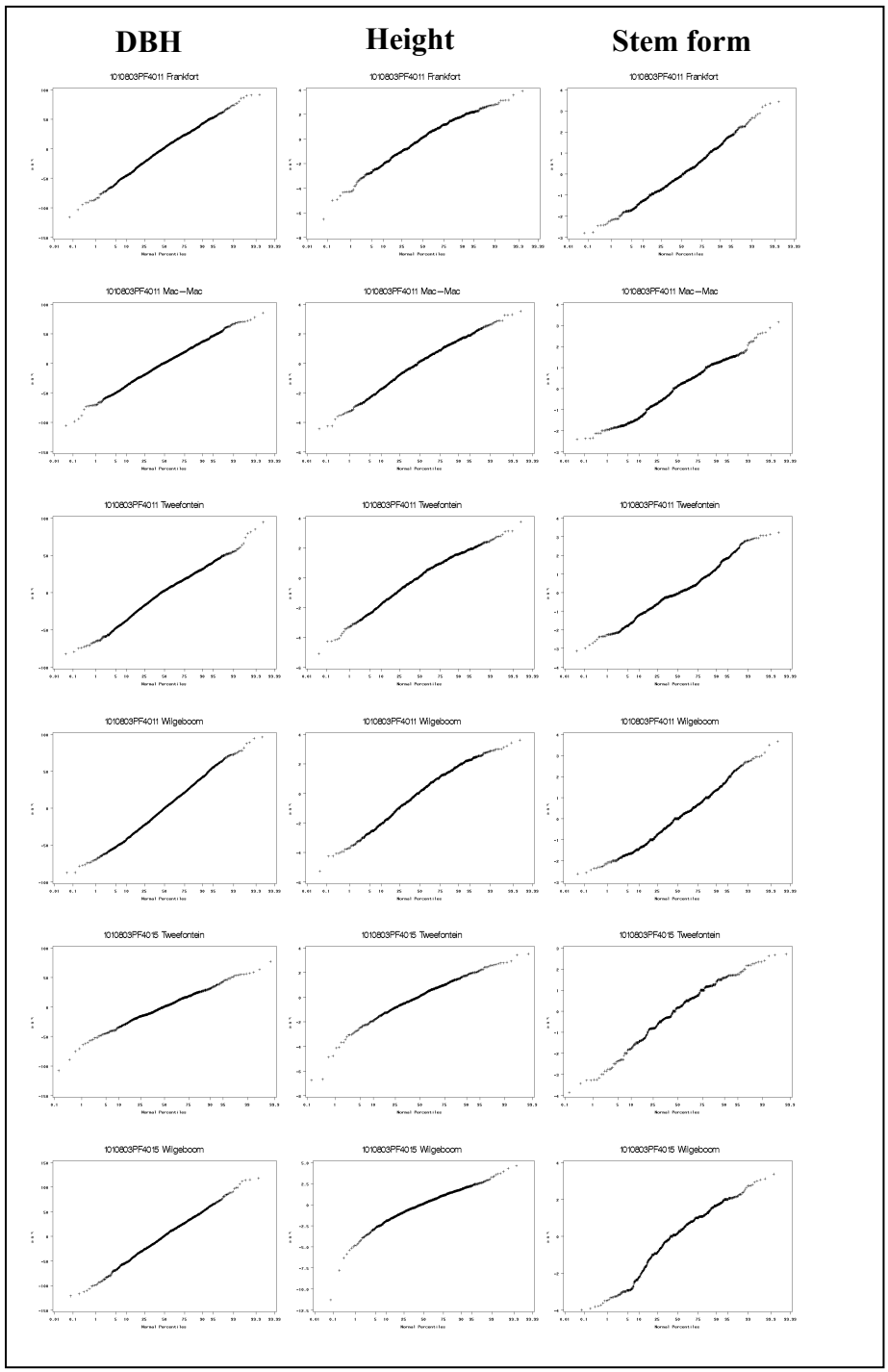

Figure 5.2 Normal probability plots for each selection trait in the F_2 *P. patula* trials.

5.2.2 Significance of family effects

The PROC GLM procedure in SAS was used to perform an analysis of variance (ANOVA) for each trait (DBH, height and stem form) in each of the *P. patula* trials used in the study.

DBH, height and stem form family effects in the F_1 trials were all significant ($\alpha = 0.05$) (Table 5.2). There were significant family effects ($\alpha = 0.05$) for DBH, height and stem form traits in all of the F_2 trials (Table 5.3).

Table 5.2 Analysis of variance for significance of family effects for each selection trait used in the study in the F_1 *P. patula* trials.

Trial	Trait	DF	F value	Pr > F
1010303PF4002.01	DBH	41	1.91	0.0006
Belfast	Height		2.24	< 0.0001
	Stem		8.90	< 0.0001
1010303PF4002.02	DBH	28	2.39	0.0002
Tweefontein	Height		4.61	< 0.0001
	Stem		2.69	< 0.0001
1010803PF4003	DBH	40	9.04	< 0.0001
Rietfontein	Height		2.70	< 0.0001
	Stem		3.01	< 0.0001
1010803PF4004	DBH	66	2.32	< 0.0001
Wilgeboom	Height		2.65	< 0.0001
	Stem		3.56	< 0.0001
1010803PF4005.01	DBH	48	2.50	< 0.0001
Wilgeboom	Height		2.48	< 0.0001
	Stem		3.58	< 0.0001
1010803PF4005.02	DBH	48	6.43	< 0.0001
Tweefontein	Height		5.89	< 0.0001
	Stem		2.39	< 0.0001
1010803PF4006.01	DBH	41	5.04	< 0.0001
Tweefontein	Height		5.46	< 0.0001
	Stem		2.82	< 0.0001

Trial	Trait	DF	F value	Pr > F
1010803PF4006.02	DBH	42	1.63	0.0070
Jessievale	Height		1.61	0.0085
	Stem		1.41	0.0463
1010803PF4007.01	DBH	41	1.62	0.0087
Jessievale	Height		1.61	0.0097
	Stem		2.07	0.0001
1010803PF4007.02	DBH	41	2.45	< 0.0001
Frankfort	Height		4.04	< 0.0001
	Stem		3.26	< 0.0001
1010803PF4008.01	DBH	284	4.24	< 0.0001
Tweefontein	Height		5.34	< 0.0001
	Stem		3.61	< 0.0001
1010803PF4008.02	DBH	48	3.34	< 0.0001
Jessievale	Height		3.53	< 0.0001
	Stem		2.44	< 0.0001
1010803PF4009	DBH	184	4.24	< 0.0001
Jessievale	Height		4.10	< 0.0001
	Stem		5.20	< 0.0001
1010803PF4010	DBH	63	2.74	< 0.0001
Jessievale	Height		4.15	< 0.0001
	Stem		3.00	< 0.0001

Table 5.3 Analysis of variance for significance of family effects for each selection trait used in the study in the F_2 *P. patula* trials.

Trial	Trait	DF	F value	Pr > F
1010803PF4011.01	DBH	88	2.22	< 0.0001
Wilgeboom	Height		2.14	< 0.0001
	Stem		2.52	< 0.0001
1010803PF4011.02	DBH	80	3.26	< 0.0001
Mac-Mac	Height		2.89	< 0.0001
	Stem		1.96	< 0.0001
1010803PF4011.03	DBH	88	2.32	< 0.0001
Tweefontein	Height		2.34	< 0.0001
	Stem		1.50	0.0024
1010803PF4011.04	DBH	63	2.21	< 0.0001
Frankfort	Height		2.17	< 0.0001
	Stem		3.04	< 0.0001
1010803PF4015.01	DBH	58	2.10	< 0.0001
Tweefontein	Height		2.12	< 0.0001
	Stem		1.44	0.0273
1010803PF4015.02	DBH	58	2.06	< 0.0001
Wilgeboom	Height		2.13	< 0.0001
	Stem		2.09	< 0.0001

5.3 Estimation of genetic parameters

5.3.1 Estimation of variance components and narrow-sense heritability

The variance components and narrow-sense heritabilities for DBH, height and stem form in the F_1 and F_2 *P. patula* trials were estimated and then used in the prediction of the BLUP selection indices.

Harvey's Mixed Model Least-Squares and Maximum Likelihood programme was used to obtain the variance and covariance component estimates required for calculating the narrow-sense heritabilities. The family (σ_f^2) and environmental (σ_e^2) (error) components of variance for each F_1 and F_2 trial are presented in Tables 5.4 and 5.5.

The among family covariance components and the error variance estimates between the selection traits in each trial are presented in Table A5 and Table A6 in Appendix A.

Table 5.4 Family and environmental variance component estimates for the three selection traits used in the study in the F_1 *P. patula* trials.

Trial	DBH		Height		Stem form	
	σ_f^2	σ_e^2	σ_f^2	σ_e^2	σ_f^2	σ_e^2
1010303PF4002.01 Belfast	0.0110	0.9593	0.0310	0.9375	0.0368	0.9213
1010303PF4002.02 Tweefontein	0.0041	0.9315	0.1735	0.7636	0.0609	0.8407
1010803PF4003 Rietfontein	0.1677	0.8087	0.0341	0.8765	0.0322	0.7428
1010803PF4004 Wilgeboom	0.0642	0.9386	0.0676	0.9287	0.0765	0.7606
1010803PF4005.01 Wilgeboom	0.0646	0.9174	0.0612	0.9208	0.0941	0.7708
1010803PF4005.02 Tweefontein	0.1833	0.7819	0.1708	0.7861	0.0418	0.7632
1010803PF4006.01 Tweefontein	0.0719	0.9129	0.0815	0.9146	0.0165	0.8386
1010803PF4006.02 Jessievale	0.0225	0.9423	0.0272	0.9334	0.0131	0.8585
1010803PF4007.01 Jessievale	0.0165	0.9734	0.0067	0.9712	0.0217	0.8978
1010803PF4007.02 Frankfort	0.0726	0.8794	0.1340	0.8257	0.0977	0.8124
1010803PF4008.01 Tweefontein	0.0724	09250	0.0862	0.9118	0.0448	0.7144
1010803PF4008.02 Jessievale	0.0689	0.9243	0.0781	0.9125	0.0280	0.7174
1010803PF4009 Jessievale	0.0704	0.9178	0.0582	0.9306	0.0886	0.7900
1010803PF4010 Jessievale	0.0371	0.9573	0.0590	0.9336	0.0168	0.8772

Table 5.5 Family and environmental variance component estimates for the three selection traits used in the study in the F_2 *P. patula* trials.

Trial	DBH		Height		Stem form	
	σ_f^2	σ_e^2	σ_f^2	σ_e^2	σ_f^2	σ_e^2
1010803PF4011.01 Wilgeboom	0.0739	0.8948	0.0574	0.8548	0.0729	0.8018
1010803PF4011.02 Mac-Mac	0.1051	0.8577	0.0880	0.8131	0.0449	0.8126
1010803PF4011.03 Tweefontein	0.0777	0.8909	0.0688	0.8345	0.0231	0.8370
1010803PF4011.04 Frankfort	0.0706	0.8875	0.0617	0.8450	0.0996	0.7804
1010803PF4015.01 Tweefontein	0.0854	0.8199	0.0883	0.7999	0.0392	0.8122
1010803PF4015.02 Wilgeboom	0.0670	0.8787	0.0877	0.8483	0.0894	0.7912

The narrow-sense heritability estimates for the selection traits, DBH, height and stem form in the F_1 and F_2 trials were calculated with Harvey's Mixed Model Least-Squares and Maximum Likelihood programme (Tables 5.6 and 5.7). In the F_1 trials the individual heritabilities ranged from 0.017 to 0.760 for DBH and ranged from 0.283 to 0.436 in the F_2 trials. Heritabilities for height ranged from 0.027 to 0.740 in the F_1 trials and 0.252 to 0.398 in the F_2 trials. Heritabilities for stem form ranged from 0.060 to 0.435 in the F_1 trials and from 0.107 to 0.453 in the F_2 trials.

Table 5.6 Narrow-sense heritability estimates for selection traits (DBH, height and stem form) in each F_1 *P. patula* trial used in the study.

	DBH		**Height**		**Stem form**	
Trial	**h^2**	**std error**	**h^2**	**std error**	**h^2**	**std error**
1010303PF4002.01 Belfast	0.045	0.051	0.128	0.067	0.154	0.072
1010303PF4002.02 Tweefontein	0.017	0.119	0.740	0.243	0.270	0.170
1010803PF4003 Rietfontein	0.687	0.166	0.150	0.062	0.166	0.066
1010803PF4004 Wilgeboom	0.256	0.083	0.272	0.085	0.365	0.099
1010803PF4005.01 Wilgeboom	0.263	0.101	0.249	0.099	0.435	0.131
1010803PF4005.02 Tweefontein	0.760	0.174	0.714	0.168	0.208	0.088
1010803PF4006.01 Tweefontein	0.292	0.078	0.327	0.084	0.077	0.033
1010803PF4006.02 Jessievale	0.093	0.054	0.113	0.058	0.060	0.047
1010803PF4007.01 Jessievale	0.067	0.052	0.027	0.043	0.095	0.059
1010803PF4007.02 Frankfort	0.305	0.122	0.558	0.165	0.429	0.144
1010803PF4008.01 Tweefontein	0.291	0.034	0.345	0.038	0.236	0.029
1010803PF4008.02 Jessievale	0.277	0.090	0.315	0.097	0.150	0.065
1010803PF4009 Jessievale	0.285	0.044	0.235	0.039	0.403	0.055
1010803PF4010 Jessievale	0.149	0.046	0.238	0.064	0.075	0.030

Table 5.7 Narrow-sense heritability estimates for selection traits (DBH, height and stem form) in each F_2 *P. patula* trial used in the study.

Trial	DBH		Height		Stem form	
	h^2	std error	h^2	std error	h^2	std error
1010803PF4011.01 Wilgeboom	0.305	0.083	0.252	0.077	0.334	0.086
1010803PF4011.02 Mac-Mac	0.436	0.095	0.390	0.090	0.209	0.068
1010803PF4011.03 Tweefontein	0.321	0.080	0.305	0.078	0.107	0.054
1010803PF4011.04 Frankfort	0.295	0.097	0.272	0.094	0.453	0.117
1010803PF4015.01Tweefontein	0.377	0.171	0.398	0.173	0.184	0.147
1010803PF4015.02 Wilgeboom	0.283	0.103	0.375	0.116	0.406	0.121

5.3.2 Phenotypic correlations between selection traits

The phenotypic correlations between the three selection traits, DBH, stem form and height in the F_1 trials used in the forward prediction runs, was calculated in SAS. The Pearson correlation coefficients between these traits for each F_1 trial and for the combined set of F_1 trials are presented in Table 5.8. The largest correlations were observed between the DBH and height traits. At the $\alpha = 0.05$ level of significance the correlation coefficients were significant except for two in trial 1010803PF4003 at Rietfontein.

Table 5.8 Pearson correlation coefficients between selection traits in the F_1 *P. patula* trials.

Trial	n	Phenotypic Correlation		
		DBH-Height	DBH-Stem form	Height-Stem form
1010303PF4002.01 Belfast	904	0.59731^{***}	0.13065^{***}	0.10053^{**}
1010303PF4002.02 Tweefontein	291	0.66764^{***}	0.23588^{***}	0.19893^{**}
1010803PF4003 Rietfontein	1571	0.50260^{***}	0.03293^{ns}	0.02591^{ns}
1010803PF4004 Wilgeboom	1343	0.60978^{***}	0.08547^{**}	0.08150^{**}
1010803PF4005.01 Wilgeboom	922	0.64141^{***}	0.13061^{***}	0.23831^{***}

Trial	n	Phenotypic Correlation DBH-Height	DBH-Stem form	Height-Stem form
1010803PF4005.02 Tweefontein	980	0.67022***	-0.13595***	-0.11016***
1010803PF4006.01 Tweefontein	2414	0.81044***	0.29213***	0.28136***
1010803PF4006.02 Jessievale	1177	0.76988***	0.21497***	0.19117***
1010803PF4007.01 Jessievale	1165	0.76370***	0.27621***	0.27112***
1010803PF4007.02 Frankfort	687	0.65732***	0.31933***	0.32307***
1010803PF4008.01 Tweefontein	11413	0.68535***	0.31016***	0.28366***
1010803PF4008.02 Jessievale	1451	0.71835***	0.31000***	0.30397***
1010803PF4009 Jessievale	6595	0.69716***	0.24451***	0.25257***
1010803PF4010 Jessievale	2997	0.71275***	0.31389***	0.26815***
Combined F_1 trials	33910	0.69034***	0.24684***	0.23612***

Correlation coefficient significant effect: *** p<0.0001 ** p<0.01 * p<0.05 ns non-significant at p = 0.05

5.4 Predicted breeding values

Forward prediction BLUP breeding values were used to predict the individual breeding values within the F_1 *P. patula* population of trials. Multiple-site, multiple-trait forward prediction scenarios were run in both Matgen programmes (Delphi and Clipper versions) using the forward prediction model (as described in section 3.5.4 in Chapter 3). In Delphi Matgen four scenarios, one for each of the three different matrix inversion techniques and adapted ridge regression, were run for each economic weighting set (see Table 3.1 for description of economic weighting sets) which gave a total of 10 runs per scenario. In Clipper Matgen two scenarios were run, one with the full pivoting and the other with the partial pivoting matrix inversion technique and were run with each economic weighting set (see Table 3.1 for description of economic weighting sets) also giving a total of 10 runs per scenario. Multiple-site, single-trait forward prediction scenarios were run in both Matgen programmes to compare with the multiple-trait scenarios. Ridge regression was not applied as a collinearity mitigation method for the single-trait scenarios, as these models are simpler and less likely to display collinearity.

5.4.1 The choice of k values for adapted ridge regression

The k values that were used for the adapted ridge regression runs in the F_1 *P. patula* trials were either zero (where no collinearity was detected) or ranged from 0.01 to 0.09 (in increments of 0.01; where various levels of severity of collinearity were detected) for each family at each site.

5.4.2 Instability

In the multiple-site, multiple-trait scenarios, the number of instability cases detected by Matgen (Delphi and Clipper versions) in the forward prediction data sets varied with the different economic weightings. There was no specific pattern in the number of instability cases detected over the range of economic weightings. The levels of instability and where it was detected in the F_1 *P. patula* runs is summarised in Table 5.9.

The Clipper Matgen indicated a substantially higher number of instability cases than the higher precision Delphi Matgen. The highest number of cases of instability were detected in the partial pivoting Clipper runs (ranging in instability in individuals from 385 (67.4%) families to individuals from 567 (99%) families). The full pivoting technique in the Clipper Matgen also had high numbers of instability cases but slightly less than in the partial pivoting technique (ranging in instability in individuals from 344 (60.2%) families to individuals from 563 (98.6%) families).

In the Delphi Matgen programme the highest number of cases of instability were detected in the partial pivoting technique (ranging in instability in individuals from 122 (21.4%) families to individuals in 157 (27.5%) families), followed by the adapted ridge regression technique (ranging in instability in individuals from 92 (16.1%) families to individuals in 143 (25%) families). Only a few cases of instability were detected in the full pivoting and SVD techniques in Delphi Matgen (ranging in instability in individuals from one family to instability in individuals from five families).

In the multiple-site, single-trait scenarios few instability cases were detected for the different matrix inversion techniques in Delphi and Clipper Matgen programmes. Where instability was detected, the most cases were detected for the partial pivoting technique in Clipper Matgen with the height trait having instability in individuals from 15 families, Stem form trait having instability in individuals from 10 families and the DBH trait having instability in individuals from four families. In Delphi Matgen only the partial pivoting technique for the height trait had cases of instability in individuals from 14 families.

Table 5.9 Instability levels detected in the F_1 *P. patula* forward selection runs in Matgen.

Economic weighting set No.	**Number of instability cases detected by Matgen**	**Forward prediction method**					
		PP	**FP**	**SVD**	**RIDGE**	**Low PP**	**Low FP**
1	Families	133	3	3	92	390	384
	Individuals	3872	106	106	2555	26234	25084
2	Families	126	3	2	98	500	500
	Individuals	3704	87	87	2469	31555	31449
3	Families	142	5	5	114	502	502
	Individuals	4006	155	155	3037	32420	32492
4	Families	157	5	5	143	517	517
	Individuals	4326	155	155	3639	32740	32812
5	Families	151	3	3	115	515	515
	Individuals	4219	81	81	3062	32708	32780
6	Families	143	3	3	133	403	389
	Individuals	4054	81	81	3674	25098	23759
7	Families	122	1	1	115	384	344
	Individuals	3628	37	37	3279	24817	22905
8	Families	131	3	3	102	500	500
	Individuals	3784	87	87	2763	31987	31605
9	Families	149	3	3	130	515	515
	Individuals	4160	81	81	3352	32708	32780

Economic weighting set No.	Number of instability cases detected by Matgen	Forward prediction method					
		PP	FP	SVD	RIDGE	Low PP	Low FP
10	Families	155	5	5	139	567	570
	Individuals	4311	137	137	3867	32395	32072

Total number of families in the F_1 *P. patula* forward selection runs was 571

Total number of individuals in the F_1 *P. patula* forward selection runs was 33920

PP = partial pivoting high precision control; FP = full pivoting high precision; SVD = singular value decomposition; RIDGE = adapted ridge regression; low PP = partial pivoting low precision in Clipper Matgen; low FP = full pivoting low precision in Clipper Matgen

Indicators of instability in the methods:

- Wrong sign coefficients and high correlations between predicted and true values
- Very large condition numbers observed
- In the inversions of the V matrix where values may be too large or too small and cause problems in the inversion
- Examining the matrix calculated from the product of the phenotypic covariance matrix with its inverse, for deviations from the expected identity pattern

5.4.3 Effect of instability on population parameters

The standard deviations of the forward predicted breeding values ($\hat{g}_{fwd}$) were calculated in SAS and were found to be high to very high for most of the F_1 *P. patula* population scenarios (Table A12 in Appendix A). Standard deviations for the partial pivoting technique (Delphi) exceeded 100. The range in mean standard deviation values among techniques for the remaining methods (excluding the Delphi partial pivoting technique) ranged from 1.72 to 3.68 across economic weighting scenarios in the F_1 *P. patula* population data.

The measures of deviation from normality of $\hat{g}_{fwd}$ (e.g. kurtosis and skewness) in the *P. patula* F_1 population scenarios were high (Table A12 in appendix A). Mean values for kurtosis exceeded 481 and values for skewness ranged from 7.30 to 23.96 across economic weighting scenarios in the F_1 *P. patula* population data.

Examination of the forward prediction matrices in the *P. patula* data revealed differences between the Clipper and Delphi Matgen inversion matrices. For Delphi Matgen a number of large value off-diagonal elements were identified for certain families in the identity matrices (product of the V matrix with the V^{-1} matrix). These were mainly in the runs using the partial pivoting technique. The off-diagonal elements should all be zero or very close to zero. These families also had large and in some cases very large breeding values ($\hat{g}_{fwd}$). The phenotypic V matrices in Clipper and Delphi Matgen were compared and these were found to be identical in all cases (example family is shown in Figure 5.4). Comparison of the $\hat{g}_{fwd}$ values in the merged data sets, that were used in the correlations between the predicted and realised breeding performance, showed that for the different matrix inversion techniques used, the $\hat{g}_{fwd}$ values were either the same or very similar for most of the data sets. A small proportion of values had large differences and most of these were found between the partial pivoting techniques with the rest of the matrix inversion techniques. In these cases, the higher numerical precision of Delphi Matgen results in elements of the inverse matrix which are very small numbers compared to the same elements in the lower precision Clipper which become zero (see example of family P1098 in the *P. patula* F_1 trials in Figure 5.4) and also more cases of large off-diagonal elements in the intended identity matrix where the values should also be zero. Family P1098 in the *P. patula* F_1 trials for example had a very large $\hat{g}_{fwd}$ value of 185.273 for the partial pivoting matrix inversion technique of Delphi Matgen compared to the range of 0.374 to 0.593 for the other matrix inversion techniques across the two programmes (shown in Figure 5.3). A number of large off-diagonal elements were observed in the intended identity matrix of this family and more were observed in Delphi Matgen than in the Clipper Matgen programme (as shown in Figure 5.5).

Family	Site	Trial	g_hat56f	g_hatsvdf	g_hatgaussf	g_hatr56f	g_hat5nf	g_hat5ngssf
SP48	4	wilg004	0.541	0.541	0.541	0.523	0.541	0.541
P317	10	jess007	0.020	0.020	0.020	-0.005	0.02	0.02
P299	10	jess007	0.021	0.021	0.021	0.011	0.021	0.021
P1075	13	jess009	0.248	0.248	0.248	0.288	0.248	0.248
SP52	9	frank007	0.841	0.834	0.834	0.812	0.841	0.834
.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.
SP49	4	wilg004	0.335	0.335	0.335	0.300	-13.497	0.335
SP61	4	wilg004	3.243	0.443	0.443	0.447	21.047	0.443
P407	11	jess008	-20.257	0.568	0.595	0.630	0.595	0.696
P81	7	mac006	-0.089	0.532	0.532	0.510	-22.646	-0.229
P294	9	frank007	43.250	0.396	0.396	0.414	0.396	0.396
P1098	11	jess008	185.273	0.461	0.593	0.506	0.374	0.593

Figure 5.3 Example family in the *P. patula* trials with large $\hat{g}_{fwd}$ values. The large $\hat{g}_{fwd}$ value for the family (P1098) is circled in red. The columns are the following: g_hat56f = Delphi partial pivoting; g_hatsvdf = singular value decomposition; g_hatgaussf = Delphi full pivoting; g_hatr56f = Delphi ridge regression; g_hat5nf = Clipper partial pivoting and g_hat5ngssf = Clipper full pivoting.

Delphi Matgen partial pivoting (showing part of the matrices):

Matrices

Family P1098 on site 11 | print | next

Matrix with determinant = 3.63183475540026E-10

0.993153	0.112893	0.2659	0.0402786	0.716776	0.094269	0.0688803	-0.00188761	0.0528884
0.112893	0.112893	0.0402786	0.0402786	0.094269	0.094269	0.0688803	-0.00188761	0.0528884
0.2659	0.0402786	0.745406	0.0621648	0.26309	0.0376694	-0.00188761	0.0280028	-0.00072221
0.0402786	0.0402786	0.0621648	0.0621648	0.0376694	0.0376694	-0.00188761	0.0280028	-0.00072221
0.716776	0.094269	0.26309	0.0376694	0.990614	0.121584	0.0528884	-0.00072221	0.0781324
0.094269	0.094269	0.0376694	0.0376694	0.121584	0.121584	0.0528884	-0.00072221	0.0781324
0.0688803	0.0688803	-0.00188761	-0.00188761	0.0528884	0.0528884	0.0961671	0.00507395	0.0690349
-0.00188761	-0.00188761	0.0280028	0.0280028	-0.00072221	-0.00072221	0.00507395	0.0631339	0.00562235
0.0528884	0.0528884	-0.00072221	-0.00072221	0.0781324	0.0781324	0.0690349	0.00562235	0.109575

Inverted matrix

2.33777	-1640.38	-0.240029	536.725	-1.61234	-690.148	-430.198	-16.9717	-464.929
-2.33777	-193.858	0.240029	1980.15	1.61234	225.475	1315.72	-52.38	8.08189
-0.240029	11091.4	1.62524	-3634.17	-0.249638	4684.17	2912.88	114.916	3148.05
0.240029	-8574.56	-1.62524	283.987	0.249638	-4125.96	-4137.03	-23.3244	-2499.79
-1.61234	-1702.01	-0.249638	558.213	2.37042	-721.825	-447.421	-17.6512	-483.543
1.61234	1237.33	0.249638	0	-2.37042	682.667	682.667	0	341.333
-5.45808E-18	885.521	4.8062E-20	-1224.15	7.99668E-17	235.245	-391.356	30.3017	201.845
1.70379E-19	-69.3517	-2.44163E-20	91.5912	-6.20802E-18	-17.6512	30.3017	30.7983	-27.424
2.7754E-18	456.848	-6.55404E-21	648.255	-4.15791E-17	-142.21	201.845	-27.424	-78.0642

DOS-based Clipper Matgen partial pivoting :

```
DOS partial pivoting
family= P1098
Number of sites=          14.000000
V=
 0.993153  0.112893  0.265900  0.040279  0.716776  0.094269  0.068880 -0.001888  0.052888
 0.112893  0.112893  0.040279  0.040279  0.094269  0.094269  0.068880 -0.001888  0.052888
 0.265900  0.040279  0.745406  0.062165  0.263090  0.037669 -0.001888  0.028003 -0.000722
 0.040279  0.040279  0.062165  0.062165  0.037669  0.037669 -0.001888  0.028003 -0.000722
 0.716776  0.094269  0.263090  0.037669  0.990614  0.121584  0.052888 -0.000722  0.078132
 0.094269  0.094269  0.037669  0.037669  0.121584  0.121584  0.052888 -0.000722  0.078132
 0.068880  0.068880 -0.001888 -0.001888  0.052888  0.052888  0.096167  0.005074  0.069035
-0.001888 -0.001888  0.028003  0.028003 -0.000722 -0.000722  0.005074  0.063134  0.005622
 0.052888  0.052888 -0.000722 -0.000722  0.078132  0.078132  0.069035  0.005622  0.109575
 0.068880  0.068880 -0.010069 -0.010069  0.058075  0.058075  0.070363 -0.010069  0.052888
-0.010069 -0.010069  0.028003  0.028003 -0.022544 -0.022544 -0.010069  0.044815 -0.022544
 0.058075  0.058075 -0.022544 -0.022544  0.058201  0.058201  0.052888 -0.022544  0.058201

Inversion of v
family= P1098
 2.337775 -40.833349   -0.240029  56.555908  -1.612341  7.467552    12.781774   2.429047
-2.337775 -1793.393097  0.240029  2460.303838 1.612341 -472.138208  872.734563 -71.780331
-0.240029  260.894066   1.625238 -382.940790 -0.249638 -39.396072  -86.545558  -16.447110
 0.240029  2255.965680 -1.625238 -2967.227498 0.249638  597.605280 -1137.598606 108.037798
-1.612341 -38.424351   -0.249638  58.820045   2.370420  3.719197    13.293475   2.526291
 1.612341 -426.246305   0.249638  499.389163 -2.370420 -42.876847   221.950739 -20.177340
 0.000000  885.516337   0.000000 -1224.144164 0.000000  235.244213 -391.353530  30.301528
 0.000000 -69.351284    0.000000  91.590688   0.000000 -17.651049   30.301528   30.798336
 0.000000 -456.845437   0.000000  648.252100  0.000000 -142.209005  201.843827 -27.423912
 0.000000 -200.658459   0.000000  272.319912  0.000000 -55.102457   67.815239  -11.022159
 0.000000 -596.628647   0.000000  791.093449  0.000000 -127.437698  293.262446 -35.209617
 0.000000  2089.539943  0.000000 -2796.423287 0.000000  472.872136 -1002.457997 96.945643
```

Figure 5.4 V matrix and inverted V matrix for family P1098 in the *P. patula* trials. The red circled values in the Figure show an example of where the higher precision Delphi produces values (although very small) compared to the lower precision Clipper where these same values become zero.

Delphi Matgen partial pivoting (showing part of the matrix):

Product of V-matrix with it's inverse

1	0	-7.10958E-21	-2.77556E-17	1.3095E-19	-3.29597E-17	3.1225E-17	-8.67362E-19	1.9082E-17
7.21069E-21	1	-3.72144E-21	-1.38778E-17	2.25294E-20	1.73472E-18	3.46945E-18	0	-8.67362E-18
-5.67455E-17	6824.35	1	-2235.09	-2.29191E-16	2881.99	1792.28	70.7069	1936.97
-7.86833E-21	3.46945E-18	-6.49106E-21	1	-5.83039E-20	4.0766E-17	-1.73472E-18	-1.0842E-18	6.93889E-18
-5.58385E-20	-1.11022E-16	-3.77353E-20	-1.38778E-17	1	5.37764E-17	6.93889E-18	-4.33681E-19	8.67362E-18
-1.51809E-20	0	-3.85394E-21	1.249E-16	-1.08334E-20	1	9.02056E-17	-3.90313E-18	-5.20417E-18
3.20423E-21	3.46945E-17	2.87311E-21	-1.38778E-17	-6.39336E-22	-5.20417E-18	1	4.33681E-19	1.73472E-18
5.16319E-21	-1.04083E-17	-5.98521E-21	2.42861E-17	-1.657E-20	0	-3.46945E-18	1	-5.20417E-18
-4.0597E-21	5.55112E-17	4.4618E-21	4.16334E-17	2.68425E-20	1.04083E-17	3.46945E-17	-2.60209E-18	1

DOS-based Clipper Matgen partial pivoting:

```
Family= P1098
Inversion multiplied with original v
1.000000 0.000000   0.000000  0.000000   0.000000  0.000000   0.000000  0.000000  0.000000
0.000000 1.000000   0.000000  0.000000   0.000000  0.000000   0.000000  0.000000  0.000000
0.000000 160.378970 1.000000 -234.621324 0.000000 -24.393783 -53.250997 -10.119815 13.979412
0.000000 0.000000   0.000000  1.000000   0.000000  0.000000   0.000000  0.000000  0.000000
0.000000 0.000000   0.000000  0.000000   1.000000  0.000000   0.000000  0.000000  0.000000
0.000000 0.000000   0.000000  0.000000   0.000000  1.000000   0.000000  0.000000  0.000000
0.000000 0.000000   0.000000  0.000000   0.000000  0.000000   1.000000  0.000000  0.000000
0.000000 0.000000   0.000000  0.000000   0.000000  0.000000   0.000000  1.000000  0.000000
0.000000 0.000000   0.000000  0.000000   0.000000  0.000000   0.000000  0.000000  1.000000
0.000000 0.000000   0.000000  0.000000   0.000000  0.000000   0.000000  0.000000  0.000000
0.000000 0.000000   0.000000  0.000000   0.000000  0.000000   0.000000  0.000000  0.000000
0.000000 0.000000   0.000000  0.000000   0.000000  0.000000   0.000000  0.000000  0.000000
```

Figure 5.5 Product of V matrix and inverted V matrix (identity matrix) for family P1098 in the *P. patula* trials. The red circled values show the example in this family where the off-diagonal elements of the identity matrix are large values and not the expected zero values. These values are also shown to be larger values in the higher precision Delphi compared to the lower precision Clipper.

5.5 Realised breeding performance

Realised breeding performance, the performance of the parents of the next generation, was estimated by backward prediction in the F_2 *P. patula* trials data set. Scenarios using the partial pivoting, full pivoting and singular value decomposition (SVD) matrix inversion techniques were run in the Delphi Matgen programme and partial and full pivoting matrix inversion techniques were used in runs in the Clipper Matgen programme. Runs were completed for the multiple-site single-trait and the multiple-site, multiple-trait scenarios for each set of economic weightings in both Matgen programmes. In the backward prediction runs in the Delphi Matgen programme the full

pivoting and SVD methods had correlation coefficients of r = 1 for the multiple-trait and single-trait scenarios and the two methods in the Clipper Matgen programme had correlation coefficients of r = 1 for the multiple-trait and single-trait scenarios. In Delphi Matgen for the multiple-trait scenarios the partial pivoting method had correlation coefficients of r = 0.94 with the full pivoting and with the SVD methods. The correlation coefficients between the backward runs of the Delphi Matgen and Clipper programmes with each other ranged from r = 0.90 to r = 0.94 in the multiple-trait scenarios and r = 0.98 in the single-trait scenarios. The full pivoting backward prediction runs from each programme were used further in the study for evaluating the correlations with the predicted breeding values of the F_1 generation.

5.6 Accuracy of predicted and realised breeding performance

Accuracy measures (r_{fb}) using Pearson correlation coefficients (described in section 3.7) between predicted breeding values from the F_1 forward prediction runs ($\hat{g}_{fwd}$) and breeding values from the F_2 backward prediction runs ($\hat{g}_{bwd}$) were obtained in SAS. The predicted breeding values in the F_1 trials were correlated to the realised breeding performance in the F_2 trials for the multiple-trait and the single-trait scenarios.

The accuracy (r_{fb}) between the F_1 predicted breeding values and the F_2 realised breeding performances are presented in Table 5.10 (using Delphi full pivoting backward selection for correlations) and Table 5.11 (using Clipper full pivoting backward selection for correlations). The accuracy (correlations) for the single traits are presented in Table 5.10 and Table 5.11. The mean accuracy values over the different techniques for each of the economic weighting scenarios for the F_1F_2 *P. patula* trials is also given in Table 5.10 and Table 5.11. The correlations for the multiple-trait scenarios were, however, not statistically significant at the 5% level of significance as indicated in the tables. Correlations were low and many were low and negative for the multiple-trait and single-trait scenarios. The heritability of the compound weighted trait for the F_1 trials in the tables is used as a benchmark against which the different methods are evaluated. This evaluation was made using twice the accuracy ($2r_{fb}$) (as described in section 3.9). The mean accuracy values over the ten economic weighting scenarios for the F_1F_2 *P. patula* trials is given in Table 5.12 together with the single trait correlations and compound heritabilities for further comparison.

Table 5.10 A comparison of the accuracy (r_{fb}) between the backward prediction $\hat{g}_{bwd}$ (F_2 trials and using Delphi value) and the forward prediction $\hat{g}_{fwd}$ (F_1 trials) runs with the heritability of the compound weighted trait.

	Forward Prediction Method						**2x mean accuracy across method ($2r_{fb}$)**	**Heritability of compound weighted trait h_c^2**
Economic weighting*	**Partial pivoting**	**Full pivoting**	**SVD**	**Ridge regression**	**Low Partial pivoting**	**Low Full pivoting**		
1	-0.12236^{ns}	-0.02643^{ns}	-0.00914^{ns}	-0.07367^{ns}	0.13984^{ns}	0.07042^{ns}	-0.0071	0.269
2	-0.04416^{ns}	0.10605^{ns}	-0.00151^{ns}	-0.02454^{ns}	0.16218^{ns}	0.16613^{ns}	0.1214	0.279
3	-0.08779^{ns}	0.04005^{ns}	-0.00527^{ns}	-0.03446^{ns}	0.14858^{ns}	0.13957^{ns}	0.0669	0.285
4	-0.08436^{ns}	0.06961^{ns}	0.00745^{ns}	-0.00764^{ns}	0.15015^{ns}	0.16561^{ns}	0.1003	0.292
5	0.01434^{ns}	0.18707^{ns}	-0.00148^{ns}	0.00076^{ns}	0.20479^{ns}	0.20989^{ns}	0.2051	0.275
6	-0.20328^{ns}	0.15710^{ns}	0.10324^{ns}	0.08466^{ns}	0.14783^{ns}	0.18469^{ns}	0.1581	0.242
7	-0.14219^{ns}	0.01451^{ns}	0.04238^{ns}	-0.03713^{ns}	0.13159^{ns}	0.07378^{ns}	0.0276	0.256
8	-0.03023^{ns}	0.11949^{ns}	-0.00237^{ns}	-0.02834^{ns}	0.16540^{ns}	0.16619^{ns}	0.1300	0.274
9	-0.01828^{ns}	0.18496^{ns}	0.02854^{ns}	0.01229^{ns}	0.22204^{ns}	0.20266^{ns}	0.2107	0.270
10	-0.22602^{ns}	0.22275^{ns}	0.10757^{ns}	0.13443^{ns}	0.16092^{ns}	0.23837*	0.1599	0.237
Single traits:								
DBH	-0.01343^{ns}	-0.01679^{ns}	-0.01679^{ns}		0.01336^{ns}	0.00997^{ns}	-0.00474	0.270
Height	0.10924^{ns}	0.12824^{ns}	0.12824^{ns}		0.16095^{ns}	0.16879^{ns}	0.13909	0.315
Stem form	0.26465*	0.26465*	0.26465*		0.25183*	0.26947*	0.26305	0.223

Accuracy (correlation coefficient) significant effect: *** p<0.0001 ** p<0.01 * p<0.05 ns non-significant at p = 0.05
Low = low precision in Clipper Matgen
*For a description on the economic weighting sets please refer to Table 3.1.
Significance not calculated for twice the mean correlation coefficients across techniques.

Table 5.11 Accuracy (r_{fb}) between the backward prediction $\hat{g}_{bwd}$ (F_2 trials and using Clipper value) and the forward prediction $\hat{g}_{fwd}$ (F_1 trials) runs with the heritability of the compound weighted trait.

	Forward Prediction Method						**2x mean accuracy across method ($2r_{fb}$)**	**Heritability of compound weighted trait h_c^2**
Economic weighting*	**Partial pivoting**	**Full pivoting**	**SVD**	**Ridge regression**	**Low Partial pivoting**	**Low Full pivoting**		
1	-0.08543^{ns}	-0.04749^{ns}	-0.02696^{ns}	-0.11126^{ns}	0.10587^{ns}	0.02171^{ns}	-0.0479	0.269
2	0.00355^{ns}	0.09130^{ns}	-0.01226^{ns}	-0.07185^{ns}	0.11290^{ns}	0.13548^{ns}	0.0864	0.279
3	-0.02241^{ns}	0.03999^{ns}	0.00381^{ns}	-0.05871^{ns}	0.08841^{ns}	0.10937^{ns}	0.0535	0.285
4	-0.00596^{ns}	0.07993^{ns}	0.02800^{ns}	-0.02175^{ns}	0.08249^{ns}	0.14097^{ns}	0.1012	0.292
5	0.04791^{ns}	0.17014^{ns}	-0.02631^{ns}	0.02173^{ns}	0.16637 ^{ns}	0.18668^{ns}	0.1888	0.275
6	-0.19562^{ns}	0.16154^{ns}	0.08445^{ns}	0.07635^{ns}	0.15521^{ns}	0.15558^{ns}	0.1458	0.242
7	-0.12845^{ns}	-0.00938^{ns}	0.01505^{ns}	-0.06906^{ns}	0.12596^{ns}	0.02379^{ns}	-0.0140	0.256
8	0.00752^{ns}	0.09871^{ns}	-0.02251^{ns}	-0.08552^{ns}	0.12425^{ns}	0.13461^{ns}	0.0857	0.274
9	0.01432^{ns}	0.16405^{ns}	0.00653^{ns}	-0.05372^{ns}	0.17921^{ns}	0.17636^{ns}	0.1623	0.270
10	-0.21571^{ns}	0.23280^{ns}	0.09059^{ns}	0.12650^{ns}	0.16692^{ns}	0.21281^{ns}	0.2046	0.237
Single traits:								
DBH	-0.00637^{ns}	-0.00950^{ns}	-0.00950^{ns}		0.01833^{ns}	0.01518^{ns}	0.00163	0.270
Height	0.11134^{ns}	0.12677^{ns}	0.12677^{ns}		0.14007^{ns}	0.14637^{ns}	0.13026	0.315
Stem form	0.29109*	0.29109*	0.29109*		0.28285*	0.29626*	0.29047	0.223

Accuracy (correlation coefficient) significant effect: *** p<0.0001 ** p<0.01 * p<0.05 ns non-significant at p = 0.05
Low = low precision in Clipper Matgen
*For a description on the economic weighting sets please refer to Table 3.1.
Significance not calculated for twice the mean correlation coefficients across techniques.

Table 5.12 Mean accuracy (over economic weight scenarios) and single trait accuracy ($2r_{fb}$) between the backward prediction ($\hat{g}_{bwd}$) and the forward prediction ($\hat{g}_{fwd}$) comparing collinearity mitigation techniques together with the mean compound heritability.

Scenarios	**Generation**	**Collinearity Mitigation Method used with BLUP**						**Mean heritability of compound weighted trait(h_c^2)**
		PP	**FP**	**SVD[3]**	**RR**	**Low PP**	**Low FP**	
Mean over 10 multiple-trait scenarios:	F_1F_2 *P. patula*	-0.18887	0.21503	0.05388	0.00527	0.32666	0.32346	0.268
Single traits:								
DBH	F_1F_2 *P. patula*	-0.02686^{ns}	-0.03358^{ns}	-0.03358^{ns}		0.02672^{ns}	0.01994^{ns}	0.270
Height		0.21848^{ns}	0.25648^{ns}	0.25648^{ns}		0.32190^{ns}	0.33758^{ns}	0.315
Stem form		0.52930^{*}	0.52930^{*}	0.52930^{*}		0.50366^{*}	0.53894^{*}	0.223

Accuracy (correlation coefficient) significant effect: *** p<0.0001 ** p<0.01 * p<0.05 ns non significant

Significance not calculated for twice the mean correlation coefficients among techniques over economic weighting scenarios. Accuracy is multiplied by 2 (2rfb) in order for it to be evaluated with the heritability of the compound weighted trait as explained in section 3.9.

SVD = singular value decomposition

PP = partial pivoting control; FP = full pivoting; RR = ridge regression; Low = lower precision in Clipper Matgen

In order to assess whether significant differences existed between the mean accuracies, mean r_{fb} (Table 5.9 and Table 5.10) of the different matrix inversion techniques and different numerical precision algorithms for the multiple-trait scenarios, Fisher's Least Significant Difference (LSD) multiple range tests ($\alpha = 0.05$) were run. The results of these LSD multiple range tests are presented in Table 5.13.

In this set of trial data, the LSD multiple range test ($\alpha = 0.05$) between the mean r_{fb} for each matrix inversion technique in each of the Matgen programmes (Delphi and Clipper) indicated that there was a significant difference between the partial pivoting technique (performed worst) in Delphi Matgen and the rest of the techniques in Delphi Matgen and Clipper Matgen as shown by the different letters in the LSD multiple range test for the scenario using the Delphi backward prediction (Table 5.13). When using both backwards selection techniques there was a significant difference (at $\alpha = 0.05$) between the Clipper methods (performed better) and the Delphi SVD, adapted ridge regression and partial pivoting methods. When the Delphi backward prediction was used there was also a significant difference between the Clipper methods and the full pivoting Delphi method (Table 5.13). There were no significant differences between the SVD and adapted ridge regression techniques in Delphi Matgen when correlated to either of the backward prediction scenarios. There were no significant differences between the partial pivoting Delphi Matgen technique and ridge regression in the scenario using the Clipper backwards selection. There was also no significant difference between the two Clipper methods in the scenarios using the Delphi Matgen and Clipper backwards selection for the correlations.

Table 5.13 Fisher's Least Significant Difference multiple range test for the mean accuracy (mean r_{fb}) for the F_1F_2 *P. patula* scenarios (means with the same letter are not significantly different from each other at $\alpha = 0.05$).

Scenario	Method	n	LSD	Mean r_{fb}
F_1F_2 with Delphi backward prediction	Partial pivoting Clipper	10	A	0.16333
	Full pivoting Clipper	10	A	0.16173
	Full pivoting	10	B	0.10752
	SVD	10	C	0.02694
	Ridge	10	C	0.00264
	Partial pivoting	10	D	-0.09443
F_1F_2 with Clipper backward prediction	Partial pivoting Clipper	10	A	0.13076
	Full pivoting Clipper	10	A	0.12974
	Full pivoting	10	A	0.09816
	SVD	10	B	0.01404
	Ridge	10	BC	-0.02473
	Partial pivoting	10	C	-0.05803

A further comparison was made between the mean correlations across the techniques and the compound heritabilities for each economic weight scenario for the F_1F_2 *P. patula* population data (refer to section 3.9 for an explanation for the use of this method of comparison). The *P. patula* population data (values obtained from Table 5.10) deviated from expected, with the relationship points scattered from the linear regression line (the lower right-hand side scatter in Figure 5.6). The range in compound heritability (h_c^2) was small and it was difficult to obtain a good trend line. There was, however, a large range in the correlations (r_{fb}) in the *P. patula* data where some techniques and scenarios achieved the theoretical correlation whereas many did not. Plotting the correlations of the best techniques (highest r_{fb}) in each scenario with the compound heritabilities in the *P. patula* data resulted in a better fit, with the value of twice the correlations being within the expected order of magnitude (the upper right-hand side scatter of Figure 5.6).

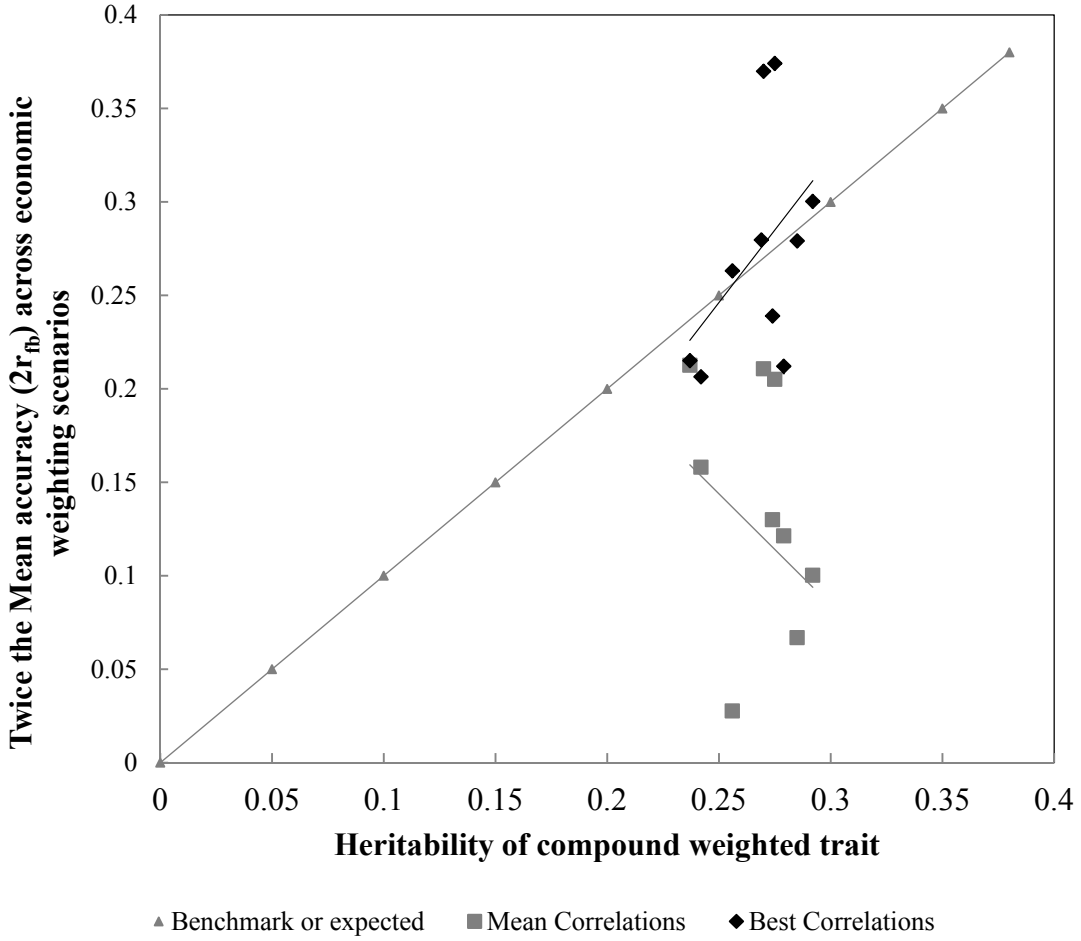

Figure 5.6 Twice the mean correlations ($2r_{fb}$) across techniques within the economic weighting scenarios and the best correlation within each economic weighting scenario relative to the heritability of the compound weighted trait across the same economic weighting scenarios for the F_1F_2 *P. patula* population data. The lines represent the linear relationships between the correlations and the heritability of the compound weighted trait.

5.7 Rank correlation comparisons

Spearman rank correlation coefficients were calculated in SAS for the forward prediction runs in the multiple-trait scenarios with the different economic weighting sets and these are presented in Table A13 in Appendix A. The rank correlations were

calculated to assess whether there were any significant rank changes in the individuals in the various forward prediction runs.

Large rank differences were observed between the Clipper Matgen partial pivoting (PP) and full pivoting (FP) methods and rank correlation coefficients ranged from 0.704 to 0.728 over the different economic weightings for the multiple-trait scenarios. The largest rank differences were observed between the partial pivoting method of Delphi Matgen and the Clipper Matgen methods. The correlation coefficients were lowest between the Delphi Matgen methods and the partial pivoting Clipper method, ranging from 0.468 to 0.551 (PP Delphi and PP Clipper), 0.699 to 0.741 (FP Delphi and PP Clipper), 0.600 to 0.658 (SVD Delphi and PP Clipper) and 0.598 to 0.641 (Ridge Delphi and PP Clipper). Small rank differences were observed between the Delphi methods of full pivoting, SVD and adapted ridge regression with correlation coefficients ranging from 0.783 to 0.871 (FP and SVD), 0.820 to 0.862 (FP and Ridge) and 0.846 to 0.885 (SVD and Ridge). Very few rank differences were observed between the two full pivoting techniques of the two programmes and ranged from 0.886 to 0.908. In the case of the single-trait scenarios no rank differences ($r = 1.000$) or only very small rank differences ($r = 0.95$ to $r = 0.99$) occurred between the different methods. All of the rank correlation coefficients were significant at $p < 0.0001$.

5.8 Realised genetic gains

The realised genetic gains, expressed in terms of standard deviation units were estimated for each economic weighting set and each of the matrix inversion techniques (partial pivoting, full pivoting and SVD) and adapted ridge regression method. The mean of the breeding values from the backward prediction runs of the F_2 *P. patula* trials were used to calculate the realised genetic gains (Ruotsalainen & Lindgren 1998; Silva *et al.* 2000) for the top and bottom 10% of the forward prediction families in the F_1 trials as described in section 3.8. The top and bottom 10% were used as opposed to the five percent that was used in the *E. grandis* scenarios because of the smaller number of observations in the pedigree data of the *P. patula* population (see section 3.8). These realised genetic gains are given in Table A14 in Appendix A.

The variance of the genetic gains (in standard deviation units) among the mitigation techniques for the *P. patula* population data is shown in Table 5.14.

Table 5.14 The variance of realised genetic gains (in standard deviation units) between techniques within scenarios in the *P. patula* population data.

Species	**Selection Population**	**Performance measured in**	**Variance of genetic gains***	
			Top %	**Bottom %**
P. patula	F_1	F_2	0.0125	0.0269
* top and bottom percentage is 10 %				

The magnitude of the improvement in realised genetic gains varied over the different economic weightings (see Table 3.1 for the economic weightings used) and differences were also found between the different matrix inversion methods (see Table A14 in Appendix A). In the F_1F_2 *P. patula* scenarios a trend of better realised gains in the lower numerical precision Clipper programme was observed and a significant ($p < 0.0001$) difference between the Clipper techniques (better) and all of the techniques of the Delphi programme except with the full pivoting Delphi technique was observed (Table A14). Full pivoting Clipper had higher realised genetic gains than the partial pivoting Clipper technique although not significantly different from each other (Table A14).

In the *P. patula* population data set, the largest difference in the realised genetic gains between the technique having the lowest gains and the technique having the highest gains in the top 10 % of families resulted in a 50 times improvement or difference of 0.3803 standard deviation units (economic weighting set five but did, however, depend on the very low gain of -0.0747 units in the Delphi partial pivoting technique) and is illustrated in Figure 5.7. The largest difference in realised genetic gains between the technique with the lowest gains and the best alternative technique in the bottom 10 % of families resulted in a 222 % improvement or a difference of 0.711 standard deviation units (economic weighting set five) and is illustrated in Figure 5.8 below. The partial pivoting Clipper method had lower gains than the best alternative technique in all of the

economic weighting sets for the realised gains in the top 10 % of families, except for in economic weighting set three and eight (Table A14). In the bottom 10 % of families the partial pivoting Clipper method had the highest gains in five out of the ten economic weighting sets (Table A14). In the top 10% of families the range in realised genetic gains among techniques within economic weighting scenarios ranged from a 0.0827 to 0.3803 difference in standard deviation units and in the bottom ten percent of families from 0.2007 to 0.711 difference (Table A14) in standard deviation units.

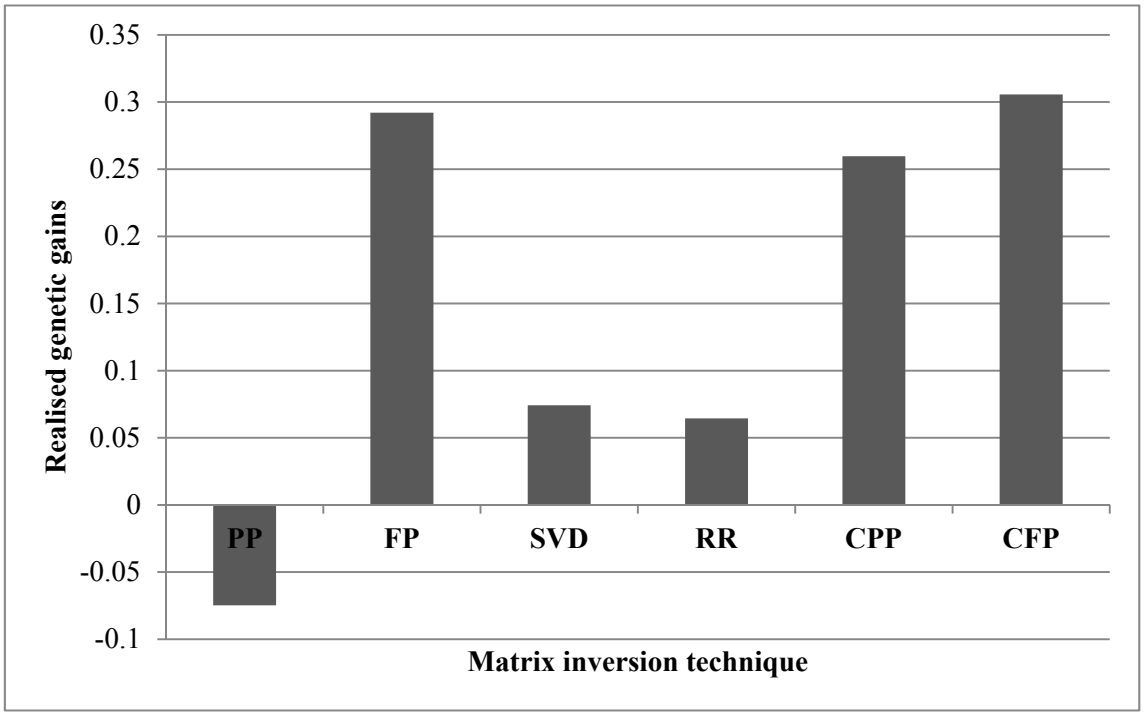

Figure 5.7 Realised genetic gains in the F_2 *P. patula* population data for economic weighting scenario five from the top 10% of F_1 breeding value selections. Techniques in higher precision Delphi: partial pivoting (PP), full pivoting (FP), singular value decomposition (SVD), ridge regression (RR) and in lower precision Clipper: partial pivoting (CPP) and full pivoting (CFP).

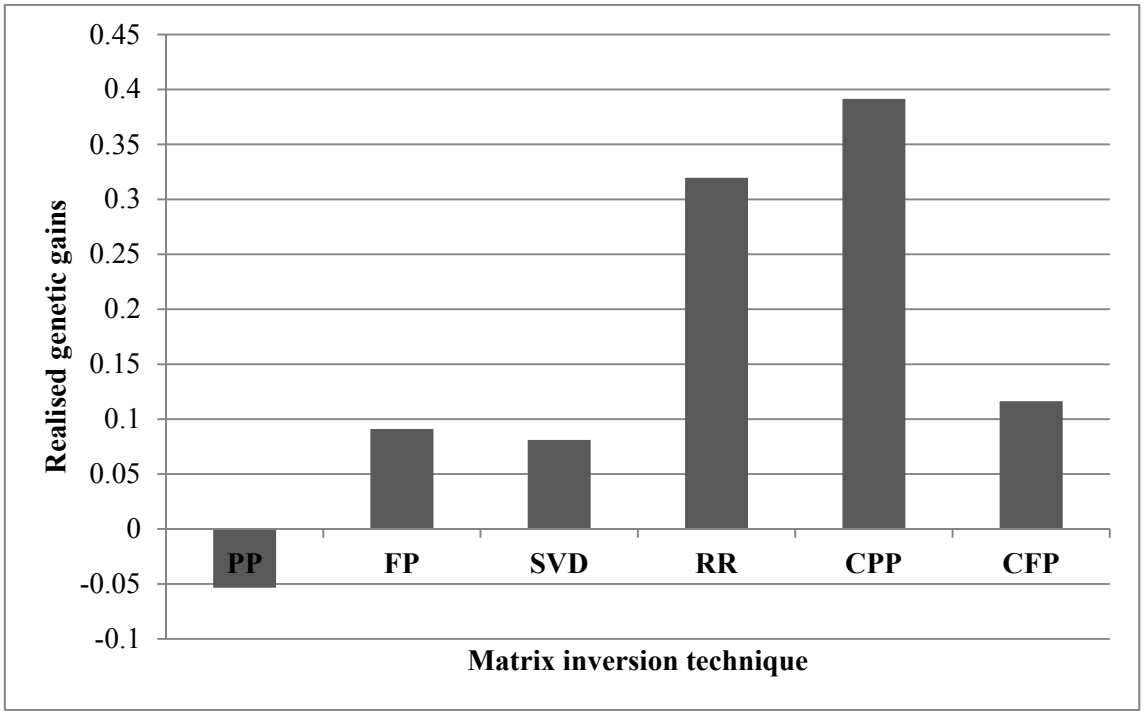

Figure 5.8 Realised genetic gains in the F_2 *P. patula* population data for economic weighting scenario five from the bottom 10% of F_1 breeding value selections. Techniques in higher precision Delphi: partial pivoting (PP), full pivoting (FP), singular value decomposition (SVD), ridge regression (RR) and in lower precision Clipper: partial pivoting (CPP) and full pivoting (CFP). The signs for the bottom 5% gains have been reversed for this plot.

An analysis of variance and a LSD multiple range test (using Proc GLM in SAS) was executed on the gains data (combination of the top and bottom 10% gains) for the *P. patula* trials for the multiple-trait scenarios. The technique effect (the different matrix inversions and adapted ridge regression) and the economic weights effect were highly significant ($p < 0.0001$) for the *P. patula* gains data. The results of the LSD multiple range test are presented in Table 5.15.

Table 5.15 Fisher's Least Significant Difference multiple range test for the mean of the top 10% and bottom 10% realised genetic gains in standard deviation units over the economic weightings for the F_1F_2 *P. patula* scenarios (means with the same letter are not significantly different from each other at $\alpha = 0.05$).

Gain scenario	**Method**	**n**	**LSD**	**Mean Gains (standard deviation units)**
F_1F_2	Full pivoting Clipper	20	A	0.15918
	Partial pivoting Clipper	20	A	0.13523
	Full pivoting	20	AB	0.09291
	SVD	20	B	0.04874
	Partial pivoting	20	C	-0.03546
	Ridge	20	C	-0.04276

CHAPTER 6
DISCUSSION OF RESULTS

Best Linear Unbiased Prediction (BLUP) is an important statistical tool for the selection of individuals for the next generation of breeding (forward prediction) or the selection of best parents (backward selection) in a tree breeding programme . In forestry, data from breeding trials are often unbalanced and messy because of the different rates of survival of families and individuals within a family in these trials (White & Hodge 1989; Furlani *et al*. 2005). The individuals of each family are related and there is an expected degree of correlation between the family means on different sites (White & Hodge 1989). Correlation between family means at different sites and correlation between selection traits may lead to collinearity in certain models on which predictions are made. A high degree of collinearity may cause problems and adversely affect the prediction of the breeding values in a selection index (Verryn 1994). It is therefore, important to know if adverse effects of collinearity on the reliability of predictions can be expected in tree breeding practice. Instability related to collinearity has been identified in simulation studies with randomly generated populations and using different predictive techniques (Simple Genetic Algorithm and Best Linear Prediction) to obtain the selection index (Verryn & Roux 1998). The studies by Verryn (1994) and Verryn and Roux (1998) revealed the need to investigate the effects and problems associated with collinearity and resultant instability in experimental data.

This study investigated the potential occurrence of instability and the possible remediation thereof in BLUP by use of different matrix inversion methods and ridge regression in tree breeding population data. The study was based on historical tree breeding data in order to allow for the use of data from multiple generations of breeding. The data for the case studies were large datasets from 39 breeding trials of three generations of pure species *E. grandis* and 20 breeding trials of two generations of pure species *P. patula*.

Multiple selection traits were chosen for the study as selection in most tree breeding programmes tends to involve multiple-trait selection (White & Hodge 1989; Cotterill & Dean 1990; Hodge & White 1992; Silva et al. 2000). The available selection traits in the breeding trials for this study were diameter at breast height (DBH), height and stem form. The stem form trait is assessed on a subjective eight point scale. After correcting for fixed effects and standardising the data, this trait was then treated as a continuous variable. A comparison with single-trait selection, of the three chosen traits, was made in order to assess whether the incidence of instability would increase as more traits were added to the selection index models.

The phenotypic correlations between the traits were calculated in order to establish whether there were any high phenotypic correlations between any of the selection traits that could contribute towards a problem of collinearity in the data set. A strong correlation between height and DBH is expected in forest tree species (Cotterill & Dean 1990). In eucalypt species, for example, in *E. urophylla*, phenotypic correlations ranging from 0.58 to 0.91 over various ages, between DBH and height have been found (Kien *et al*. 2009). In *E. grandis* correlations of 0.50 to 0.89 over different sites have been found (Kageyama & Vencovsky 1983). In pine species, for example, in *Pinus sylvestris*, Peltola *et al.* (2009) obtained phenotypic correlations between DBH and height of 0.44 and 0.55 at two sites. Similar high correlations between the three selection traits in this study were found and these were highest between DBH and height in both the *E. grandis* set of trials and the *P. patula* trials (Table 4.13 and Table 5.8). High correlations could result in a measure of collinearity (Belsey *et al.* 1980) in the analysis and as the main objective of the study was to investigate how different techniques deal with typical instability as a result of collinearity, the collinear data and models were not removed or avoided.

6.1 Predicted breeding values

The heritabilities of the three selection traits (DBH, height and stem form) were of an acceptable magnitude for use in BLUP calculations. The narrow-sense heritabilities for the three selection traits, DBH, height and stem form for the F_1, F_2 and F_3 *E. grandis* trials were generally high for both DBH and height across the trials (Table 4.10, Table

4.11 and Table 4.12). Heritabilities for the stem form trait were slightly lower than those for DBH and height in the F_1, F_2 and F_3 *E. grandis* trials (Table 4.10, Table 4.11 and Table 4.12). The heritability estimates for *E. grandis* in this study were similar to those found in other *E. grandis* studies such as DBH 0.088 - 0.307, height 0.11 - 0.256 and stem form 0.048 - 0.072 (Verryn *et al.* 1997; Snedden *et al*. 2007). Kageyama and Vencovsky, 1983 also obtained similar estimates in *E.* grandis over a number of sites and values ranged from 0.126 - 0.202 (DBH), 0.106 - 0.386 (height) and 0.281 - 0.363 (stem form). In the F_1 and F_2 *P. patula* trials the narrow-sense heritabilities for DBH, height and stem form had a large range of values from low to high values across the trials particularly in the F_1 trials (Table 5.6 and Table 5.7). Similar heritability estimates have been found in other studies in *P. patula* (DBH: 0.302 - 0337; height 3.11 - 4.11; stem form 0.414 - 0.677) by Hettasch and Verryn (1999) and (height 0.224 - 0.713 and stem form 0.239) by Ladrach and Lambeth (1991). Nyoka *et al*. (1994) also obtained similar heritability estimates of 0.19 - 0.26 for height, 0.14 - 0.16 for DBH and 0.29 - 0.32 for stem straightness.

In the three population scenarios (F_1F_2 and F_2F_3 *E. grandis* and F_1F_2 *P. patula*) the standard deviations (and variances) of the predicted breeding values ($\hat{g}_{fwd}$) were lowest in the relatively stable *E. grandis* F_1 population scenarios (Table A7 and Table A12). The standard deviations increased steadily, relative to the *E.* grandis F_1 population scenarios, as the population data became less stable in the F_2F_3 *E. grandis* and F_1F_2 *P. patula* population scenarios. In BLUP theory the variance among predictions will be larger for predictions based on high quality data (White & Hodge 1989, p288), however in the F_2F_3 *E. grandis* and F_1F_2 *P. patula* population scenarios the distributions of the predicted breeding values ($\hat{g}_{fwd}$) show more deviations from normality and this may result in inflated variances. The measures of deviation from normality of $\hat{g}_{fwd}$ (e.g. kurtosis and skewness) followed a similar pattern of increase as the population data became less stable. Kurtosis and skewness values were much closer to the expected zero level of normally distributed population data in the F_1 *E. grandis* scenarios. In the other two less stable populations' data (F_2F_3 *E. grandis* and F_1F_2 *P. patula*) these values were much higher. The relatively more stable F_1 *E. grandis* population data also had fewer $\hat{g}_{fwd}$ outliers than the scenarios of the other two population data sets.

6.2 Rank correlations

When considering the rank correlations between the forward prediction scenarios of the *E. grandis* trials there were no clear patterns for rank changes between the two Matgen programmes (Delphi and Clipper) and the different methods used within them. Differences in the number of rank changes could, however, be observed in both *P. patula* and *E. grandis* scenarios. In the F_1 *E. grandis* trials only small rank changes and in some cases no rank changes were observed within the economic weighting scenarios (Table A8) between the different methods. More rank changes were observed for the multiple-trait scenarios when comparing the Delphi Matgen methods with the Clipper Matgen methods. In the F_2 *E. grandis* population data (Table A8) more rank changes were evident. In the *P. patula* trial multiple-trait scenarios, many more rank changes were found in comparison to those in the *E. grandis* population scenarios (Table A13). More rank changes were observed in the higher precision programme than the lower precision programme in the *P. patula* scenarios. Correlations were particularly low between the two partial pivoting methods of the Delphi and Clipper programmes (Table A13). In addition to more rank changes, there was a large range in rank correlation coefficient values in the *P. patula* population scenarios.

In contrast, the single trait scenarios for the F_1 and F_2 *E. grandis* population data and the F_1F_2 *P. patula* population data, (Table A8 and Table A13) showed very few or no rank changes between matrix inversion methods (correlation coefficients of one or close to one). This illustrating that the instability was occurring within the multiple-trait scenarios and also that the *P. patula* population data had the potential of performing in a stable manner.

The higher rank correlations in the F_1 *E. grandis* (in the order of 0.9 to 1) compared to those of the other population data, highlighted the stability of the data of this population. The *P. patula* data in contrast was less stable (highlighted by the lower rank correlations between techniques with values as low as 0.5) and the discrepancy between the different techniques used in the two programmes (Delphi and Clipper Matgen) was also more pronounced in this population than in the *E. grandis* population data.

6.3 Comparison of the accuracy (inter-generational correlations) of BLUPs (r_{fb})

Examination of the accuracy (r_{fb}) (based on the definitions of White & Hodge 1989; Mrode 1996; Falconer & Mackay 1996; Postma 2006) between the predicted breeding values and the realised breeding performance in the *E. grandis* multiple-trait scenarios revealed a trend of higher r_{fb} within the higher precision Delphi Matgen programme methods compared to the lower precision Clipper Matgen programme (Table 4.16 to Table 4.19). Varying the economic weights of the three selection traits resulted in differences observed in the r_{fb} in both the F_1F_2 scenarios and the F_2F_3 scenarios for the *E. grandis* population data (Tables 4.16 to 4.18). In the F_1F_2 scenarios the ridge regression technique in Delphi Matgen produced better results (nominally higher r_{fb}) than the other Delphi techniques (five out of 10 economic weight cases) (Table 4.16). Similarly Verryn (1994) obtained superior results for a ridge regression technique in his simulation experiments. The SVD technique was the next best performing technique (Table 4.16) in this population data.

In the *E. grandis* F_2F_3 scenarios the Gauss-Jordan full pivoting method (Delphi Matgen programme) and ridge regression were the better performing methods when the Dukuduku F_3 population backwards prediction and the Silverfontein F_3 population backwards prediction were used (Table 4.17 and Table 4.18). In one economic weighting case, the partial pivoting Delphi method surprisingly had a nominally higher r_{fb} than the other methods of both programmes (Table 4.18).

In the F_2F_3 *E. grandis* scenarios the accuracy (r_{fb}) was noticeably lower than those values obtained in the F_1F_2 *E. grandis* population scenarios. The lower correlations may be due to the higher incidence of instability in the matrix calculations and resulting large inflated index ($\hat{g}_{fwd}$) values that contributed to the lower correlations with the predicted performance. There was an improvement in the magnitude of the r_{fb} after the abnormally large breeding values were removed (Table 4.17 and Table 4.18). A very similar pattern in the relative performance of the techniques as found in the complete data set was, however, observed.

In the *P. patula* population data in the multiple-trait scenarios the accuracy (r_{fb}) between the predicted breeding values and realised breeding performance, a different trend was observed compared to that observed in the *E. grandis* scenarios. In the *P. patula* population data a trend of higher correlations within the lower precision Clipper Matgen programme compared to the higher precision Delphi programme was observed for all the economic weighting cases (Table 5.10, Table 5.11 and Table 5.12). In half the economic weight cases the partial pivoting Clipper technique had higher r_{fb} than the full pivoting Clipper technique when Delphi backwards prediction index values were used (Table 5.10). When the Clipper backwards prediction index values were used the full pivoting Clipper technique performed better than the partial pivoting Clipper technique in most cases (Table 5.11). Large to very large index ($\hat{g}_{fwd}$) values were observed for the Delphi partial pivoting technique in the r_{fb} data set in the *P. patula* trials. Values greater than the absolute value of two standard deviation units were considered to be large and those greater than the absolute value of 20 standard deviation units were considered very large in comparison to the rest of the breeding values in this population data. In each economic weighting set there was at least one extreme value greater than 130 (values ranged from 133 to as large as 269) and these large values are believed to have contributed towards the low correlations between the backwards prediction runs and the partial pivoting technique.

The comparison between the accuracy (correlations) and the compound heritability in the *E. grandis* F_1F_2 population scenarios showed that the r_{fb} values obtained were of an acceptable (to high) magnitude, since they were similar in magnitude to $(½)h_c^2$ (Falconer 1989) (Table 4.16). The effect of potential bias due to historical selection in producing the F_2 *E. grandis* population was therefore assumed to be negligible in this F_1F_2 *E. grandis* population data. In the *E. grandis* F_2F_3 population scenarios and the *P. patula* scenarios there was a much larger range of r_{fb} values of which many were much smaller in magnitude than the $(½)h_c^2$ values (Tables 4.17, 4.18, Table 5.10 and Table 5.11). This may largely be due to more cases of instability in the *E. grandis* F_2F_3 and F_1F_2 *P. patula* scenarios and instability in the matrix calculations resulting in large index ($\hat{g}_{fwd}$) values that contributed to the lower accuracy in these population scenarios.

In contrast to the multiple-trait scenarios of the *P. patula* and *E. grandis* population data, the single-trait scenarios in both species had little or no collinearity effects and very few or no unstable individuals or families in the forward and backward predictions. The accuracy (r_{fb}) values for the single-trait scenarios were of a very similar magnitude over the different techniques and the two different numerical precisions (two Matgen programmes). For this set of data the results showed that when using single-trait scenarios all the matrix inversion techniques gave reasonable and reliable results.

In the results from the Fisher's Least Significant Difference (LSD) multiple range tests ($\alpha = 0.05$) in the F_1F_2 *E. grandis* and F_1F_2 *P. patula* population scenarios a significant difference between the high and low numerical precision programmes was observed (Table 4.20 and Table 5.13). In the F_2F_3 *E. grandis* population scenarios a significant difference between partial pivoting (both precisions) techniques and the rest of the techniques of both programmes was observed (Table 4.20). When examining the F_2F_3 *E. grandis* scenarios (more unstable population) it is clear that the partial pivoting technique (whether with high or low precision) should be avoided (Table 4.20). When the lower numerical precision was used the *E. grandis* population data results of this study indicated that it is beneficial to use the full pivoting matrix inversion technique (higher mean r_{fb}) and to avoid the partial pivoting matrix inversion technique.

It is of interest that the lower numerical precision methods perform better than the higher precision methods in the *P. patula* population data. The two methods used in the low numerical precision were not significantly different from each other or from the full pivoting technique of high precision Delphi Matgen programme, when the Clipper backward prediction was used (Table 5.13). When using the high numerical precision in the F_1F_2 *P. patula* population data of this study, a notable significantly poorer performance of the partial pivoting technique compared to all the other matrix inversion techniques was observed (Table 5.13) also highlighting the need to avoid the partial pivoting technique.

In summary, it is suggested, therefore, that in some cases high numerical precision may cause instability through calculations based on residual values (based on differences in the magnitude of the values as a result of differences in the rounding off and the number

of significant digits following the decimal point). In other cases high precision can be advantageous through not truncating valuable information. Secondly, partial pivoting is in no case significantly better than full pivoting for a given numerical precision. The main reason for the difference in the two types of pivoting is inherent in the method. Although partial pivoting is computationally simpler to perform, by using the full pivoting method ensures an improved numerical solution (in comparison to that obtained for partial pivoting) and a more stable numerical solution (Dekker *et al*. 1994; Urroz 2001; Olson 2009).

A further comparison was made between the mean r_{fb} across the techniques and the compound heritabilities for each economic weighting set for each population data scenario (Figures 4.5 - 4.7 for *E. grandis* and Figure 5.6 for *P. patula*). This comparison showed the stability of the *E. grandis* F_1F_2 scenarios (where $2r_{fb}$ against h_c^2 was approximately the expected relationship) and the more unstable scenarios of the F_2F_3 *E. grandis* (substantial underperformance of the $2r_{fb}$ relative to h_c^2) scenarios. The F_1F_2 *P. patula* population scenarios also deviated from expected with the relationship points scattered from the linear regression line (lower right hand scatter of Figure 5.6). The range in h_c^2 was small and it was difficult to obtain a good trend line. There was, however, a large range in the correlations in the pine data where some techniques and scenarios achieved the theoretical correlation whereas many did not. When plotting the correlations of the best techniques (highest r_{fb}) in each scenario with the compound heritabilities in the *P. patula* population data it resulted in a better fit, where twice the correlation ($2r_{fb}$) was within the expected order of magnitude (Figure 5.6). Further evidence that these predictions were able to approach stable predictions. The best techniques also had better kurtosis and variance values for the predicted breeding values ($\hat{g}_{fwd}$). The latter performance and that of the F_1F_2 *E. grandis* population data served as a confirmation that the methodology and data used here could perform according to expected genetic theory.

The fact that no one collinearity mitigation technique gave the optimal r_{fb} (benchmarked against $1/2\ h_c^2$) in all scenarios indicated that although some techniques performed better than others, there is reason to believe that there is still room for further

development and improvement of technology to mitigate the potential negative effects of collinearity.

6.4 Impact on realised genetic gains

The range in mean accuracy (r_{fb}) (F_1F_2 and F_2F_3 *E. grandis* population data) and the r_{fb} (F_1F_2 *P. patula* population data) of 0.094 to 0.182 and the LSDs indicated that the rank changes observed could have a significant effect on the realised genetic gains.

The variance of the genetic gains among mitigation techniques within scenarios (Table 4.21 and Table 5.14) showed a trend of increasing variability in genetic gains among mitigation techniques in the less stable population data of F_2F_3 *E. grandis* and F_1F_2 *P. patula* population data. The LSD multiple range test for the realised genetic gains for each economic weighting set in the different scenarios, expressed in terms of standard deviation units showed similar trends in most cases to the tests with the mean accuracy (r_{fb}) as discussed in section 6.3.

In both the F_1F_2 and F_2F_3 *E. grandis* population scenarios, the partial pivoting technique had lower realised genetic gains compared to the other techniques. In contrast to the *E. grandis* population data in the F_1F_2 *P. patula* population scenarios the lower numerical precision programme showed better realised genetic gains than the higher numerical precision programme. In the lower numerical programme the partial pivoting technique did still however have lower realised genetic gains than the full pivoting technique.

Although the absolute differences in the realised gains (standard deviation units) appeared small in these data sets, the percentage improvements between some of the alternative techniques were large. Small changes in gain could result in substantial improvement in the economic impact in the long run (Weir 1973; Todd *et al.* 1995), mainly due to the cumulative nature of genetic gains. The range in realised genetic gains among techniques within scenarios differed by up to 0.06 standard deviation units between techniques in the relatively stable F_1F_2 *E. grandis* population data, was up to 0.22 standard deviation units between techniques in the F_2F_3 *E. grandis* population data and was as much as 0.71 standard deviation units in the *P. patula* population data. The

observed differences in genetic gains in these data sets highlight the importance of exploring alternative prediction techniques in the case of instability and for effective mitigation of potential collinearity.

Comparing the realised genetic gains from the techniques, the more stable population data had a lower variability of genetic gains between mitigation techniques, than those of the unstable population datasets. The mitigation techniques also displayed greater differences in realised genetic gains in the less stable datasets (up to 0.71 standard deviation units' difference).

CHAPTER 7 CONCLUSION

7.1 Main findings

The results of this study of the accuracy of prediction of breeding values over three generations of *E. grandis* population data (39 breeding trials and 1544 families), two generations of *P. patula* population data (20 breeding trials and 762 families) with 10 scenarios each provides the first empirical evidence of the potential negative impact of collinearity in (tree) breeding, confirming the simulation studies of tree breeding data and models of Verryn (1994).

The occurrence of instability was sensitive to the economic weightings used to calculate BLUP, and to the particular nature and structure of the data. Certain families displayed instability more readily than others, and this is thought to be as a result of the different frequencies of progeny in the various trial sites in the model (as the narrow-sense heritability and economic weightings were constant for all families of a scenario). This makes the occurrence of collinearity and resulting instability potentially variable within (unbalanced) data sets. Breeding values would need to be scrutinised in order to ensure that there is no negative impact of instability in the selection process.

Collinearity mitigation techniques had a significant effect in all data sets, however, the relative performance of techniques varied from case to case, and no one technique performed best over all the scenarios. The effect of numerical precision showed that it could cause significant differences in the correlations and this indicated that it may not always be optimal to use a higher numerical precision programme for BLUP index calculations particularly when instability is present in the matrix calculations. High precision was, however, optimal for the *E. grandis* set of data in this study.

When examining the *P. patula* data forward prediction matrices, inversions and intended identity matrices (the product of the V matrix and the inverse of the V matrix, VxV^{-1}) it was clear that, when using higher numerical precision, in cases where there was a high degree of collinearity in the data for a particular family, a perfect inverse

matrix could not be obtained. This lead to large values in the off-diagonal elements of the intended identity matrix (VxV^{-1}). The identity matrix off-diagonal elements should only be zero or close to zero values. These non-zero values in turn result in very large and unstable index values (ĝ values). These high ĝ values contributed to the poor correlations with the backwards prediction ĝ values.

Full pivoting can be recommended over partial pivoting. If the performance of the best prediction technique in each scenario in the most unstable population data are considered, the r_{fb} : h_c^2 ratio recovers to the expected range, and there is an improvement in the variance and kurtosis measures.

This study indicates that BLUP can perform as expected, however, it also confirms the potential problem of instability and the consequences thereof. It is suggested that users of BLUP should take careful note of the nature of the population of predicted values (such as kurtosis, variance, outliers and other measures of normality), and should these be outside expectation, mitigation techniques such as full pivoting, Singular Value Decomposition (SVD) or the adapted ridge regression technique should be explored.

The main outcomes of this study are:

(1) Instability (and stability) was observed in the *E. grandis* and the *P. patula* breeding data.

(2) The instability can significantly affect the realised genetic gains and the accuracy (r_{fb}) (correlation between the realised and predicted performance).

(3) In some cases, where there is a large amount of collinearity, the use of a higher precision programme for BLUP calculations can both significantly increase or decrease the accuracy of the rankings.

(4) Simple single-trait models appear to be more stable.

(5) The different matrix inversion techniques especially SVD and adapted ridge regression did not perform significantly better than the full pivoting inversion technique.

(6) A recommendation can however be made that it is beneficial to use the full pivoting Gaussian elimination matrix inversion technique and should be

used in preference to the partial pivoting Gaussian elimination matrix inversion method in both high and lower numerical precision programmes.

(7) The use of full pivoting does, however, not always mitigate instability and there is room for further improvements on mitigation.

The main findings from the study were published in December 2011 in a paper in the Southern Forests :a Journal of Forest Science[1].

7.2 Recommended future research

A possible new method has been identified from the examination of the matrix inversions and formation of the identity matrix in the *P. patula* trial data of this study. The idea is to have a method that works in a similar manner to the ridge regression technique (or SVD technique) which uses a constant (k value) augmentation of the diagonal matrix. In the new method the programme would check the matrix inversions and all of the off-diagonal elements of the product of the V matrix and the inverse of the V matrix (VxV^{-1} or putative identity matrix) for values that are too large (greater than 0.5 for example). A series of k values will be tested until a k value is obtained that will no longer result in large off-diagonal values. If such a solution is not obtainable then the programme could mark those individuals as highly unstable and possibly even delete them from the overall BLUP rankings. The programming and incorporation of such a new method into Matgen and an investigation of the effectiveness of such a method for data with large amounts of collinearity and where unstable matrix inversions and identity matrices are obtained will be a valuable future investigation.

Other programs such as ASReml (Gilmour *et al.* 2009) and TREEPLAN (Kerr *et al.* 2001) could be tested in order to determine whether the findings of this study hold true when using other methodology for BLUP calculations.

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[1] Eatwell, K.A., Verryn, S.D., Roux, C.Z. and Geerthsen, P.J.M., 2011. A comparison of collinearity mitigation techniques used in predicting BLUP breeding values and genetic gains over generations. *Southern Forests: a Journal of Forest Science*, 73(3&4): 155-163.

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APPENDIX A

The among and within family covariances between diameter at breast height (DBH), height and stem form traits for the F_1, F_2 and F_3 *E. grandis* trials are presented in Tables A1, A2 ,A3 and A4 and those for the F_1 and F_2 *P. patula* trials in Tables A5 and A6.

Table A 1 Among and within family covariances for the F_1 *E. grandis* trials.

Trial		Trait	Height	Stem		Trait	Height	Stem
1010802EA6206	Among family covariance	**DBH**	0.2844	0.0595	Error covariance	**DBH**	0.4493	-0.1030
1010802EA6206		**Height**		-0.0537		**Height**		-0.0323
1010802EA6209		**DBH**	0.2504	0.0270		**DBH**	0.4246	0.2685
1010802EA6209		**Height**		0.0401		**Height**		0.1746
1010802EA6210		**DBH**	0.2671	0.1457		**DBH**	0.4748	0.1765
1010802EA6210		**Height**		0.0607		**Height**		0.2321
1010802EA6215		**DBH**	0.1833	-0.1256		**DBH**	0.6016	0.2326
1010802EA6215		**Height**		-0.0528		**Height**		0.1418
1010802EA6218		**DBH**	0.2744	0.0463		**DBH**	0.6640	0.2899
1010802EA6218		**Height**		0.0108		**Height**		0.3067
1010802EA6221		**DBH**	0.3451	0.1773		**DBH**	0.5890	0.3654
1010802EA6221		**Height**		0.1217		**Height**		0.2925

Table A 2 Among and within family covariances for the F_2 *E. grandis* trials.

Trial		Trait	Height	Stem		Trait	Height	Stem
1010802EA62A1		**DBH**	0.2734	0.1187		**DBH**	0.5116	0.1787
1010802EA62A1		**Height**		0.0570		**Height**		0.0932
1010802EA62A2		**DBH**				**DBH**		
J.D.M. Keet			0.1585	0.0513			0.4247	0.1845
1010802EA62A2		**Height**				**Height**		
J.D.M. Keet				-0.0937				0.1185
1010802EA62A2		**DBH**				**DBH**		
Kwambonambi			0.4183	0.1205			0.5705	0.2866
1010802EA62A2		**Height**				**Height**		
Kwambonambi				0.1754				0.2494
1010802EA62A3		**DBH**	0.1985	0.1450		**DBH**	0.6196	0.1979
1010802EA62A3		**Height**		0.0601		**Height**		0.1467
1010802EA62A4		**DBH**	0.1991	0.0147		**DBH**	0.4881	0.1524
1010802EA62A4		**Height**		0.0330		**Height**		0.1699
1010802EA62A5		**DBH**	0.1970	0.0963		**DBH**	0.5466	0.1568
1010802EA62A5		**Height**		0.0720		**Height**		0.1310
1010802EA62A6		**DBH**	0.1886	0.1761		**DBH**	0.4894	0.1471
1010802EA62A6		**Height**		0.0760		**Height**		0.1962

Among Family covariance | **Error covariance**

Table A 3 Among and within family covariances for the F_3 *E. grandis* trials at Dukuduku plantation.

Trial		Trait	Height	Stem		Trait	Height	Stem
1010802EA62B4		**DBH**	0.2855	0.2053		**DBH**	0.7393	0.6297
1010802EA62B4		**Height**		0.2286		**Height**		0.6073
1010802EA62B5		**DBH**	0.1282	0.0839		**DBH**	0.7569	0.5932
1010802EA62B5		**Height**		0.0909		**Height**		0.5644
1010802EA62B6		**DBH**	0.2049	0.1388		**DBH**	0.7331	0.6070
1010802EA62B6		**Height**		0.1277		**Height**		0.5914
1010802EA62B7		**DBH**	0.2323	0.2332		**DBH**	0.7271	0.6371
1010802EA62B7		**Height**		0.2015		**Height**		0.5820
1010802EA62B8		**DBH**	0.3688	0.2488		**DBH**	0.7082	0.6310
1010802EA62B8		**Height**		0.2551		**Height**		0.5835
1010802EA62B9		**DBH**	0.4743	0.3282		**DBH**	0.6407	0.5022
1010802EA62B9		**Height**		0.3564		**Height**		0.4941
1010802EA62B10		**DBH**	0.3649	0.2621		**DBH**	0.6236	0.5026
1010802EA62B10		**Height**		0.2538		**Height**		0.4543
1010802EA62B11		**DBH**	0.1479	0.1212		**DBH**	0.6414	0.4924
1010802EA62B11		**Height**		0.1233		**Height**		0.4367
1010802EA62B12		**DBH**	0.3291	0.3138		**DBH**	0.6494	0.5113
1010802EA62B12		**Height**		0.2416		**Height**		0.4251
1010802EA62B13		**DBH**	0.3055	0.1408		**DBH**	0.6710	0.5347
1010802EA62B13		**Height**		0.1622		**Height**		0.4676
1010802EA62B14		**DBH**	0.2335	0.1451		**DBH**	0.6461	0.4771
1010802EA62B14		**Height**		0.0767		**Height**		0.3987
1010802EA62B15		**DBH**	0.2559	0.1485		**DBH**	0.7599	0.6429
1010802EA62B15		**Height**		0.1619		**Height**		0.5837
1010802EA62B16		**DBH**	0.2682	0.2239		**DBH**	0.7179	0.6243
1010802EA62B16		**Height**		0.2106		**Height**		0.5669

Among family covariance | **Error covariance**

Table A 4 Among and within family covariances for the F_3 *E. grandis* trials at Silverfontein and Westfalia plantations.

Trial		Trait	Height	Stem		Trait	Height	Stem
1010802EA62B4		**DBH**	0.3483	0.1564		**DBH**	0.5885	0.2959
1010802EA62B4		**Height**		0.2031		**Height**		0.3429
1010802EA62B5		**DBH**	0.2919	0.2931		**DBH**	0.7278	0.5437
1010802EA62B5		**Height**		0.2787		**Height**		0.5083
1010802EA62B6		**DBH**	0.1800	0.1468		**DBH**	0.6300	0.2591
1010802EA62B6		**Height**		0.1054		**Height**		0.1521
1010802EA62B7		**DBH**	0.2034	0.1578		**DBH**	0.7367	0.5113
1010802EA62B7		**Height**		0.1662		**Height**		0.4933
1010802EA62B8		**DBH**	0.2447	0.2096		**DBH**	0.7434	0.5269
1010802EA62B8		**Height**		0.1940		**Height**		0.4685
1010802EA62B9		**DBH**	0.1271	0.0813		**DBH**	0.6744	0.1654
1010802EA62B9		**Height**		0.0536		**Height**		0.1596
1010802EA62B10		**DBH**	0.1236	0.0421		**DBH**	0.8009	0.5191
1010802EA62B10		**Height**		0.0548		**Height**		0.4637
1010802EA62B11		**DBH**	0.2087	0.1649		**DBH**	0.7792	0.6262
1010802EA62B11		**Height**		0.1439		**Height**		0.5854
1010802EA62B12		**DBH**	0.1689	0.1249		**DBH**	0.7925	0.6403
1010802EA62B12		**Height**		0.1423		**Height**		0.5848
1010802EA62B13		**DBH**	0.1792	0.1042		**DBH**	0.7861	0.6280
1010802EA62B13		**Height**		0.1331		**Height**		0.5646
1010802EA62B14		**DBH**	0.1785	0.0834		**DBH**	0.7853	0.6067
1010802EA62B14		**Height**		0.0732		**Height**		0.5853
1010802EA62B15		**DBH**	0.1993	0.1462		**DBH**	0.6102	0.5785
1010802EA62B15		**Height**		0.0709		**Height**		0.4731
1010802EA62B16		**DBH**	0.3094	0.2512		**DBH**	0.6359	0.5790
1010802EA62B16		**Height**		0.2496		**Height**		0.5180

Among family covariance | **Error covariance**

Table A 5 Among and within family covariances for the F_1 *P. patula* trials.

Trial		Trait	Height	Stem		Trait	Height	Stem
1010303PF4002 Belfast		**DBH**	0.0783	0.0236		**DBH**	0.5502	0.1116
1010303PF4002 Belfast		**Height**		-0.0303		**Height**		0.1363
1010303PF4002 Tweefontein		**DBH**	0.2097	0.0432		**DBH**	0.6017	0.1600
1010303PF4002 Tweefontein		**Height**		0.0432		**Height**		0.1837
1010803PF4003 Rietfontein		**DBH**	0.2856	0.1325		**DBH**	0.4025	-0.0038
1010803PF4003 Rietfontein		**Height**		0.0107		**Height**		0.0191
1010803PF4004 Wilgeboom		**DBH**	0.2013	-0.0065		**DBH**	0.5558	0.0759
1010803PF4004 Wilgeboom		**Height**		0.0247		**Height**		0.0660
1010803PF4005 Wilgeboom		**DBH**	0.2134	0.1125		**DBH**	0.5787	0.0973
1010803PF4005 Wilgeboom		**Height**		0.1314		**Height**		0.1934
1010803PF4005 Mac-Mac	**Among family covariance**	**DBH**	0.6469	-0.0907	**Error covariance**	**DBH**	0.4804	-0.1046
1010803PF4005 Mac-Mac		**Height**		-0.0766		**Height**		-0.0753
1010803PF4006 Mac-Mac		**DBH**	0.2465	0.0433		**DBH**	0.7424	0.2635
1010803PF4006 Mac-Mac		**Height**		0.0546		**Height**		0.2542
1010803PF4006 Jessievale		**DBH**	0.0666	0.0239		**DBH**	0.7219	0.1813
1010803PF4006 Jessievale		**Height**		0.0293		**Height**		0.1479
1010803PF4007 Frankfort		**DBH**	0.3424	0.1938		**DBH**	0.5261	0.2444
1010803PF4007 Frankfort		**Height**		0.2969		**Height**		0.2137
1010803PF4007 Jessievale		**DBH**	0.0606	-0.0457		**DBH**	0.7360	0.2706
1010803PF4007 Jessievale		**Height**		-0.0215		**Height**		0.2581
1010803PF4008 Jessievale		**DBH**	0.2526	0.1160		**DBH**	0.6536	0.2369
1010803PF4008 Jessievale		**Height**		0.1056		**Height**		0.2367
1010803PF4008 Tweefontein		**DBH**	0.2116	-0.0076		**DBH**	0.6297	0.2715
1010803PF4008 Tweefontein		**Height**		-0.0029		**Height**		0.2474
1010803PF4009 Jessievale		**DBH**	0.2323	-0.0403		**DBH**	0.6256	0.2334
1010803PF4009 Jessievale		**Height**		-0.0902		**Height**		0.2527
1010803PF4010 Jessievale		**DBH**	0.1628	0.0040		**DBH**	0.6678	0.2936
1010803PF4010 Jessievale		**Height**		0.0004		**Height**		0.2516

Table A 6 Among and within family covariances for the F_2 *P. patula* trials.

Trial		Trait	Height	Stem		Trait	Height	Stem
1010803PF4015 Wilgeboom	Among Family covariance	**DBH**	0.2254	0.0039	Error covariance	**DBH**	0.5102	0.1481
1010803PF4015 Wilgeboom		**Height**		0.0273		**Height**		0.1539
1010803PF4015 Tweefontein		**DBH**	0.3013	0.0270		**DBH**	0.4529	0.1077
1010803PF4015 Tweefontein		**Height**		-0.0528		**Height**		0.0771
1010803PF4011 Tweefontein		**DBH**	0.2507	0.0960		**DBH**	0.6810	0.1884
1010803PF4011 Tweefontein		**Height**		0.1093		**Height**		0.1868
1010803PF4011 Wilgeboom		**DBH**	0.2507	0.0960		**DBH**	0.6810	0.1884
1010803PF4011 Wilgeboom		**Height**		0.1093		**Height**		0.1868
1010803PF4011 Frankfort		**DBH**	0.2470	0.1951		**DBH**	0.6792	0.1476
1010803PF4011 Frankfort		**Height**		0.1859		**Height**		0.1782
1010803PF4011 Mac-Mac		**DBH**	0.3818	0.0578		**DBH**	0.6464	0.0433
1010803PF4011 Mac-Mac		**Height**		0.0292		**Height**		0.0741

Table A 7 Measures of the deviation from normality for the predicted breeding values ($\hat{g}_{fwd}$) of the F_1 and F_2 *E. grandis* populations.

		F_1 *E. grandis* population							**F_2 *E. grandis* population**						
Economic weight*	**Measure**	**PP**	**FP**	**SVD**	**Ridge**	**Low PP**	**Low FP**	**Mean across methods**	**PP**	**FP**	**SVD**	**Ridge**	**Low PP**	**Low FP**	**Mean across methods**
1	Variance	0.0719	0.0719	0.0721	0.0707	0.0760	0.0741	0.0728	8.0805	0.0668	0.0664	0.0692	5.4939	0.0664	2.3072
	Kurtosis	0.1667	0.1666	0.2023	0.2055	0.6721	0.0824	0.2493	117.2795	1.0757	-0.0327	1.0206	67.9892	1.0820	31.4024
	Skewness	-0.1200	-0.1201	-0.1080	-0.1252	-0.1634	-0.0547	-0.1152	-5.2682	-0.0254	-0.0327	-0.0946	-4.5747	-0.0307	-1.6710
	Std deviation	0.2682	0.2682	0.2686	0.2660	0.2757	0.2722	0.2698	2.8426	0.2585	0.2577	0.2630	2.3439	0.2577	1.0372
2	Variance	0.1013	0.1013	0.1013	0.0997	0.1079	0.1041	0.1026	0.1288	0.0875	0.0867	0.0907	0.1187	0.0868	0.0999
	Kurtosis	0.0799	0.0798	0.0798	0.0927	0.6572	0.0011	0.1651	13.2618	0.8705	0.8642	0.8827	4.7666	0.8618	3.5846
	Skewness	-0.0675	-0.0676	-0.0676	-0.0752	-0.1479	-0.0214	-0.0745	1.0740	-0.0356	-0.0468	-0.0672	0.4168	-0.0449	0.2161
	Std deviation	0.3183	0.3182	0.3182	0.3157	0.3285	0.3227	0.3203	0.3588	0.2958	0.2945	0.3012	0.3445	0.2946	0.3149
3	Variance	0.1032	0.1032	0.1032	0.1016	0.1083	0.1057	0.1042	2.5502	0.0787	0.0778	0.0842	1.7606	0.0779	0.7716
	Kurtosis	0.1256	0.1256	0.1256	0.1396	0.2388	0.0421	0.1329	113.2720	1.2027	1.1826	1.2203	63.9134	1.1787	30.3283
	Skewness	-0.0345	-0.0345	-0.0345	-0.0424	-0.0414	0.0154	-0.0286	5.1951	-0.0589	-0.0747	-0.0853	4.3042	-0.0730	1.5346
	Std deviation	0.3213	0.3213	0.3213	0.3188	0.3292	0.3251	0.3228	1.5969	0.2805	0.2790	0.2902	1.3269	0.2791	0.6754
4	Variance	0.1194	0.1194	0.1194	0.1174	0.1253	0.1217	0.1204	11.6063	0.0847	0.0836	0.0911	7.9047	0.0836	3.3090
	Kurtosis	0.1455	0.1455	0.1455	0.1548	0.2120	0.0617	0.1442	118.3953	1.2962	1.2560	1.2935	68.5884	1.2519	32.0136
	Skewness	-0.0048	-0.0048	-0.0048	-0.0140	-0.0261	0.0389	-0.0026	5.3471	-0.0559	-0.0749	-0.0787	4.5618	-0.0733	1.6043
	Std deviation	0.3455	0.3455	0.3455	0.3426	0.3540	0.3489	0.3470	3.4068	0.2910	0.2891	0.3018	2.8115	0.2892	1.2316
5	Variance	0.1128	0.1128	0.1128	0.1106	0.1222	0.1160	0.1145	0.2702	0.1087	0.1079	0.1092	0.2172	0.1079	0.1535
	Kurtosis	0.1068	0.1066	0.1066	0.1177	1.5018	0.0344	0.3290	40.2360	0.6280	0.6292	0.5865	15.4087	0.6280	9.6861
	Skewness	-0.0782	-0.0784	-0.0784	-0.0911	-0.2788	-0.0413	-0.1077	-2.2839	0.0082	0.0007	-0.0315	-1.5783	0.0026	-0.6470
	Std deviation	0.3358	0.3358	0.3358	0.3325	0.3496	0.3406	0.3384	0.5198	0.3296	0.3285	0.3304	0.4661	0.3285	0.3838
6	Variance	0.0500	0.0500	0.0500	0.0479	0.0588	0.0629	0.0533	111.8793	0.0626	0.0626	0.0557	75.8379	0.0626	31.3268
	Kurtosis	0.2518	0.2516	0.2516	0.3538	3.1434	0.2103	0.7438	119.5028	0.8636	0.8641	0.3258	69.8191	0.8653	32.0401
	Skewness	-0.2031	-0.2031	-0.2031	-0.2023	0.0734	-0.1532	-0.1486	-5.3597	0.1512	0.1519	-0.0462	-4.6492	0.1541	-1.5997
	Std deviation	0.2236	0.2236	0.2236	0.2189	0.2426	0.2508	0.2305	10.5773	0.2502	0.2502	0.2360	8.7085	0.2502	3.3787

Economic weight*	Measure	F_1 *E. grandis* population							F_2 *E. grandis* population						
		PP	**FP**	**SVD**	**Ridge**	**Low PP**	**Low FP**	**Mean across methods**	**PP**	**FP**	**SVD**	**Ridge**	**Low PP**	**Low FP**	**Mean across methods**
7	Variance	0.0583	0.0583	0.0583	0.0569	0.0638	0.0601	0.0593	41.9937	0.0660	0.0658	0.0640	28.4678	0.0659	11.7872
	Kurtosis	0.3017	0.3015	0.3015	0.3790	1.6079	0.2243	0.5193	119.1416	0.8706	0.8796	0.6432	69.5425	0.8793	31.9928
	Skewness	-0.1996	-0.1997	-0.1997	-0.2039	-0.3370	-0.1345	-0.2124	-5.3429	0.0477	0.0462	-0.0808	-4.6391	0.0482	-1.6535
	Std deviation	0.2415	0.2415	0.2415	0.2385	0.2525	0.2452	0.2434	6.4803	0.2569	0.2565	0.2529	5.3355	0.2566	2.1398
8	Variance	0.0974	0.0974	0.0974	0.0958	0.1044	0.1003	0.0988	0.8259	0.0905	0.0899	0.0923	0.5865	0.0899	0.2958
	Kurtosis	0.1013	0.1012	0.1012	0.1206	1.0609	0.0239	0.2515	92.8909	0.7602	0.7609	0.7458	48.3821	0.7592	24.0498
	Skewness	-0.0903	-0.0905	-0.0905	-0.0987	-0.2146	-0.0431	-0.1046	-4.3701	-0.0178	-0.0265	-0.0585	-3.5958	-0.0245	-1.3489
	Std deviation	0.3121	0.3121	0.3121	0.3095	0.3231	0.3167	0.3143	0.9088	0.3009	0.2998	0.3038	0.7658	0.2998	0.4798
9	Variance	0.1105	0.1105	0.1105	0.1081	0.1204	0.1138	0.1123	2.2627	0.1139	0.1132	0.1128	35.5159	0.1133	6.3720
	Kurtosis	0.1629	0.1627	0.1627	0.1830	2.1212	0.0906	0.4805	106.2967	0.5749	0.5806	0.4903	68.6698	0.5800	29.5321
	Skewness	-0.0962	-0.0964	-0.0964	-0.1117	-0.3523	-0.0579	-0.1352	-4.8580	0.0296	0.0241	-0.0214	4.5701	0.0261	-0.0382
	Std deviation	0.3325	0.3325	0.3325	0.3288	0.3470	0.3373	0.3351	1.5042	0.3375	0.3365	0.3358	5.9595	0.3365	1.4684
10	Variance	0.0504	0.0504	0.0504	0.0479	0.0615	0.0509	0.0519	146.2874	0.0620	0.0620	0.0534	99.1705	0.0620	40.9495
	Kurtosis	0.0973	0.0971	0.0971	0.1802	5.2342	0.1012	0.9679	119.5689	0.9231	0.9213	0.2525	69.8657	0.9230	32.0757
	Skewness	-0.1625	-0.1625	-0.1625	-0.1533	0.5423	-0.1624	-0.0435	-5.3631	0.1941	0.1946	-0.0144	-4.6509	0.1967	-1.5738
	Std deviation	0.2245	0.2245	0.2245	0.2188	0.2480	0.2256	0.2276	12.0949	0.2490	0.2490	0.2310	9.9584	0.2491	3.8386

*For a description on the economic weighting sets please refer to Table 3.1.

PP = Partial pivoting in Delphi Matgen; FP = Full pivoting in Delphi Matgen; SVD = singular value decomposition in Delphi Matgen;
RIDGE = Adapted ridge regression in Delphi Matgen; Low PP = Partial pivoting in Clipper Matgen; Low FP = Full pivoting in Clipper Matgen

Table A 8 Spearman rank correlation coefficients for the different mitigation techniques in the forward prediction runs of the F_1 and F_2 *E. grandis* trials.

Methods	Trials	Single traits			Economic weighting*									
		DBH	Height	Stem form	1	2	3	4	5	6	7	8	9	10
PP–FP	F1	1.000	1.000	0.999	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	F2	1.000	1.000	1.000	0.936	0.962	0.944	0.944	0.946	0.950	0.946	0.938	0.941	0.949
PP–SVD	F1	1.000	1.000	0.999	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	F2	1.000	1.000	1.000	0.937	0.962	0.944	0.945	0.946	0.950	0.946	0.939	0.942	0.949
PP–RIDGE	F1				0.997	0.998	0.998	0.998	0.998	0.995	0.996	0.998	0.997	0.994
	F2				0.913	0.938	0.906	0.897	0.933	0.914	0.920	0.922	0.929	0.908
PP–Low PP	F1	0.935	0.943	0.937	0.944	0.937	0.940	0.938	0.933	0.935	0.938	0.937	0.933	0.934
	F2	0.908	0.897	0.944	0.922	0.943	0.919	0.915	0.940	0.914	0.918	0.932	0.816	0.912
PP–Low FP	F1	0.935	0.943	0.937	0.952	0.944	0.945	0.943	0.942	0.933	0.951	0.945	0.942	0.943
	F2	0.908	0.897	0.944	0.936	0.961	0.944	0.944	0.946	0.949	0.946	0.939	0.942	0.949
FP–SVD	F1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	F2	1.000	1.000	1.000	0.999	0.999	0.999	0.999	0.999	1.000	0.999	0.999	0.999	1.000
FP–RIDGE	F1				0.997	0.998	0.998	0.998	0.998	0.995	0.996	0.998	0.997	0.994
	F2				0.976	0.977	0.966	0.959	0.985	0.974	0.980	0.981	0.987	0.971
FP–Low PP	F1	0.935	0.943	0.937	0.944	0.937	0.940	0.938	0.933	0.935	0.938	0.937	0.932	0.934
	F2	0.908	0.897	0.944	0.922	0.961	0.933	0.923	0.945	0.915	0.916	0.935	0.895	0.914
FP–Low FP	F1	0.935	0.943	0.937	0.952	0.945	0.945	0.943	0.942	0.933	0.951	0.945	0.942	0.943
	F2	0.908	0.897	0.944	0.998	0.999	0.999	0.999	0.998	0.999	0.998	0.999	0.999	0.999
SVD–RIDGE	F1				0.997	0.998	0.998	0.998	0.998	0.995	0.996	0.998	0.997	0.994
	F2				0.977	0.977	0.966	0.959	0.985	0.975	0.981	0.982	0.988	0.971
SVD–Low PP	F1	0.935	0.943	0.937	0.944	0.937	0.940	0.938	0.933	0.936	0.938	0.937	0.932	0.934
	F2	0.908	0.897	0.944	0.923	0.962	0.934	0.923	0.946	0.915	0.917	0.936	0.895	0.914
SVD–Low FP	F1	0.935	0.943	0.937	0.952	0.945	0.945	0.943	0.942	0.933	0.951	0.945	0.942	0.943
	F2	0.908	0.897	0.944	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999	0.999
RIDGE–Low PP	F1				0.938	0.933	0.934	0.933	0.929	0.925	0.929	0.932	0.928	0.923
	F2				0.900	0.939	0.898	0.880	0.932	0.881	0.892	0.919	0.892	0.876
RIDGE–Low FP	F1				0.948	0.942	0.942	0.940	0.938	0.928	0.946	0.942	0.938	0.935
	F2				0.976	0.977	0.966	0.958	0.985	0.974	0.980	0.981	0.987	0.971
Low PP–Low FP	F1	1.000	1.000	1.000	0.991	0.991	0.993	0.994	0.990	0.974	0.985	0.991	0.990	0.990
	F2	0.908	0.897	0.944	0.923	0.963	0.934	0.924	0.946	0.916	0.917	0.937	0.896	0.914

Correlation coefficient significant effect: all rank correlations significant $p < 0.0001$.
PP = Partial pivoting in Delphi Matgen; FP = Full pivoting in Delphi Matgen; SVD = singular value decomposition in Delphi Matgen; RIDGE = Adapted ridge regression in Delphi Matgen;
Low PP = Partial pivoting in Clipper Matgen; Low FP = Full pivoting in Clipper Matgen; *For a description on the economic weighting sets please refer to Table 3.1

Table A 9 Realised genetic gains in standard deviation units for the F_1F_2 *E. grandis* population scenario.

Economic weighting*	Method															
	Partial pivoting		Full pivoting		SVD[1]		SVD[2]		SVD[3]		Ridge regression		Low Partial pivoting		Low Full pivoting	
	T 5 %	B 5%	T 5 %	B 5%	T 5 %	B 5%	T 5 %	B 5%	T 5 %	B 5%	T 5 %	B 5%	T 5 %	B 5%	T 5 %	B 5%
1	0.1016	-0.0731	0.1016	-0.0731	0.1016	-0.0731	0.1016	-0.0731	0.1015	-0.0690	0.1186	-0.0731	0.0838	-0.0504	0.1016	-0.0731
2	0.1353	-0.1153	0.1353	-0.1153	0.1353	-0.1153	0.1353	-0.1153	0.1503	-0.0902	0.1194	-0.1153	0.1353	-0.0826	0.1353	-0.1153
3	0.1413	-0.1619	0.1413	-0.1619	0.1413	-0.1619	0.1413	-0.1619	0.1413	-0.1706	0.1509	-0.1619	0.1413	-0.1231	0.1413	-0.1619
4	0.1598	-0.1958	0.1598	-0.1958	0.1598	-0.1958	0.1598	-0.1958	0.1571	-0.2046	0.1649	-0.1958	0.1612	-0.1958	0.1612	-0.1958
5	0.1652	-0.1115	0.1598	-0.1115	0.1598	-0.1115	0.1652	-0.1115	0.1652	-0.1115	0.1480	-0.1115	0.1652	-0.0726	0.1598	-0.1115
6	0.0760	-0.1153	0.0760	-0.1153	0.0760	-0.1153	0.0760	-0.1153	0.0402	-0.1146	0.0806	-0.1153	0.0464	-0.0885	0.0630	-0.1237
7	0.0436	-0.1139	0.0544	-0.1139	0.0544	-0.1139	0.0544	-0.1139	0.0656	-0.0528	0.0847	-0.1139	0.0544	-0.0746	0.0544	-0.0969
8	0.1173	-0.0969	0.1173	-0.0969	0.1173	-0.0969	0.1173	-0.0969	0.1379	-0.0786	0.1031	-0.0969	0.1078	-0.0643	0.1078	-0.0969
9	0.1347	-0.1189	0.1411	-0.1189	0.1411	-0.1189	0.1411	-0.1189	0.1851	-0.1429	0.1741	-0.1189	0.1411	-0.0870	0.1411	-0.1189
10	0.0608	-0.1037	0.0608	-0.1037	0.0608	-0.1037	0.0608	-0.1037	0.0543	-0.0896	0.0709	-0.1037	0.0617	-0.0760	0.0709	-0.1037

T 5% = Realised genetic gains for the Top 5%

B 5% = Realised genetic gains for the bottom 5%

SVD[1] = SVD with threshold of $1x10^{-6}$; SVD[2] = SVD with threshold of $1x10^{-2}$; SVD[3] = SVD with threshold of $1x10^{-1}$

Low = low precision in Clipper Matgen

*For a description on the economic weighting sets please refer to Table 3.1.

Table A 10 Realised genetic gains in standard deviation units for the F_2F_3 *E. grandis* population scenario at Dukuduku.

Economic weighting*	Method											
	Partial pivoting		Full pivoting		SVD*		Ridge regression		Low Partial pivoting		Low Full pivoting	
	T 5 %	B 5%	T 5 %	B 5%	T 5 %	B 5%	T 5 %	B 5%	T 5 %	B 5%	T 5 %	B 5%
1	0.0617	0.0117	0.1284	-0.1037	0.1284	-0.0562	0.0115	-0.0466	0.0106	0.0202	0.1284	-0.0562
2	-0.0050	-0.1065	0.1083	-0.0758	0.1083	-0.0758	0.0091	-0.0816	0.0465	-0.1052	0.1083	-0.0808
3	-0.0046	-0.1138	0.1008	-0.1184	0.1008	-0.1184	0.0196	-0.0684	0.0334	-0.0122	0.1008	-0.1184
4	-0.0135	-0.0543	0.0265	-0.1266	0.0265	-0.1266	0.0014	-0.0897	0.0175	-0.0803	0.0265	-0.1266
5	0.0514	-0.0192	0.1502	-0.0635	0.1502	-0.0635	0.0854	-0.0635	0.0333	0.0232	0.1502	-0.0635
6	0.0442	0.0627	0.1064	0.0187	0.1064	0.0187	0.1094	-0.0692	0.0005	0.0541	0.1064	0.0187
7	0.0738	0.0380	0.0738	-0.0740	0.0738	-0.0740	0.0511	-0.0668	0.0226	0.0455	0.0738	-0.0740
8	0.0059	0.0152	0.1320	-0.0764	0.1482	-0.0764	0.0389	-0.0518	0.0091	0.0561	0.1320	-0.0820
9	0.0919	0.0312	0.1552	-0.0583	0.1552	-0.0283	0.1369	-0.0088	0.0324	-0.0219	0.1552	-0.0283
10	0.0108	0.0733	0.0748	-0.0354	0.0748	-0.0354	0.1478	-0.1373	0.0044	0.0777	0.0748	-0.0354

T 5% = Realised genetic gains for the Top 5%
B 5% = Realised genetic gains for the bottom 5%
Low = low precision in Clipper Matgen
* SVD with threshold of $1x10^{-6}$
*For a description on the economic weighting sets please refer to Table 3.1.

Table A 11 Realised genetic gains in standard deviation units for the F_2F_3 *E. grandis* population scenario at Silverfontein.

Economic weighting*	Method											
	Partial pivoting		Full pivoting		SVD*		Ridge regression		Low Partial pivoting		Low Full pivoting	
	T 5 %	B 5%	T 5 %	B 5%	T 5 %	B 5%	T 5 %	B 5%	T 5 %	B 5%	T 5 %	B 5%
1	0.1137	0.1136	0.1006	-0.0866	0.1006	-0.1404	0.0529	-0.0833	0.0718	-0.0403	0.1006	-0.0866
2	0.1449	-0.1169	0.0945	-0.1013	0.0945	-0.1013	0.0869	-0.1198	0.1232	-0.0967	0.0945	-0.0946
3	0.1430	-0.1213	0.0903	-0.0687	0.0903	-0.0687	0.0994	-0.0911	0.0813	-0.0030	0.0903	-0.0687
4	0.1411	-0.1040	0.0755	-0.0756	0.0755	-0.0756	0.0843	-0.0731	0.0950	-0.0400	0.0755	-0.0756
5	0.0655	-0.0117	0.0708	-0.1343	0.0708	-0.1343	0.1378	-0.1343	0.0888	-0.0422	0.0708	-0.1343
6	0.0690	0.1807	0.0579	-0.0412	0.0579	-0.0412	0.0436	-0.0628	0.0568	0.0924	0.0579	-0.0412
7	0.0936	0.1675	0.1007	-0.1073	0.1007	-0.1073	0.0793	-0.0864	0.0815	0.0802	0.1007	-0.1073
8	0.0826	0.0014	0.0915	-0.1242	0.1158	-0.1242	0.1139	-0.1300	0.0591	-0.0552	0.1158	-0.1177
9	0.0850	0.0584	0.0691	-0.1384	0.0691	-0.1335	0.1286	-0.1229	0.0887	0.0136	0.0691	-0.1384
10	0.0648	0.1870	0.0500	0.0309	0.0500	0.0309	0.0563	-0.0299	0.0613	0.1268	0.0500	0.0309

T 5% = Realised genetic gains for the Top 5%
B 5% = Realised genetic gains for the bottom 5%
Low = low precision in Clipper Matgen
* SVD with threshold of $1x10^{-6}$
*For a description on the economic weighting sets please refer to Table 3.1.

Table A 12 Measures of the deviation from normality for the predicted breeding values ($\hat{g}_{fwd}$) of the F_1 *P. patula* populations.

		F_1 *P. patula* population							
Economic weight*	**Measure**	**PP**	**FP**	**SVD**	**Ridge**	**Low PP**	**Low FP**	**Mean across methods**	**Mean variance and std deviation (excluding PP)**
1	Variance	4.59E+78	0.706148	0.707817	1.338019	58.37966	0.728214	7.642E+77	12.3720
	Kurtosis	956.919307	499.7849	496.7294	1359.206	507.2819	471.3752	715.216135	
	Skewness	30.8881948	19.45819	19.33605	35.58347	19.86529	18.60982	23.95683545	
	std deviation	2.14131E+39	0.840326	0.841319	1.156728	7.640658	0.853355	3.56885E+38	2.2665
2	Variance	5.91E+78	1.092437	1.095728	0.333859	89.84202	1.137595	9.84445E+77	18.7003
	Kurtosis	956.919346	246.8796	245.4133	692.638	672.426	227.9766	507.0421453	
	Skewness	30.8881952	4.015089	4.020707	21.95429	24.08151	3.820034	14.79663694	
	std deviation	2.43036E+39	1.045197	1.04677	0.577805	9.478503	1.066581	4.05061E+38	2.6430
3	Variance	6.13E+78	1.268244	1.272532	0.204673	146.4514	1.307149	1.02177E+78	30.1008
	Kurtosis	956.919355	418.043	414.5729	367.129	692.9309	394.5165	540.6852893	
	Skewness	30.8881953	16.06895	15.9908	14.27007	24.56951	15.38822	19.52929127	
	std deviation	2.47601E+39	1.126163	1.128066	0.452408	12.10171	1.143306	4.12668E+38	3.1903
4	Variance	6.80E+78	1.61372	1.619624	0.115919	203.1358	1.661291	1.13294E+78	41.6293
	Kurtosis	956.919277	405.5868	401.9554	33.88371	708.8958	383.5542	481.7991953	
	Skewness	30.8881944	15.18451	15.13462	2.891622	24.8525	14.56838	17.25330417	
	std deviation	2.60723E+39	1.270323	1.272645	0.340468	14.25257	1.288911	4.34538E+38	3.6850
5	Variance	6.04E+78	1.590868	1.591731	0.351303	59.41783	1.663953	1.00613E+78	12.9231
	Kurtosis	956.919357	319.8295	319.3677	607.7528	563.6828	292.0142	509.9277375	
	Skewness	30.8881953	-9.4283	-9.13724	19.94092	20.33127	-8.78226	7.3020971	
	std deviation	2.45698E+39	1.261296	1.261638	0.592708	7.708296	1.289943	4.09497E+38	2.4228

		F_1 *P. patula* population							
Economic weight*	**Measure**	**PP**	**FP**	**SVD**	**Ridge**	**Low PP**	**Low FP**	**Mean across methods**	**Mean variance and std deviation (excluding PP)**
6	Variance	2.34E+78	0.786222	0.792051	6.673923	40.4091	0.807683	3.90587E+77	9.8938
	Kurtosis	956.919307	324.6432	319.7522	1520.745	131.5415	308.2957	593.6494033	
	Skewness	30.8881947	15.11105	14.60517	38.63585	6.377932	14.54722	20.02756711	
	std deviation	1.53086E+39	0.886692	0.889973	2.583394	6.356815	0.898712	2.55143E+38	2.3231
7	Variance	3.53E+78	0.418004	0.41889	3.182995	23.7426	0.433564	5.88358E+77	5.6392
	Kurtosis	956.919357	356.8061	355.0785	1479.506	112.2662	332.9512	598.9211948	
	Skewness	30.8881954	15.05315	14.84229	37.86316	6.856375	14.29478	19.96632429	
	std deviation	1.87887E+39	0.646532	0.647217	1.784095	4.872638	0.658456	3.13145E+38	1.7218
8	Variance	5.62E+78	1.022721	1.024331	0.510563	63.26584	1.06933	9.37263E+77	13.3786
	Kurtosis	956.919361	229.5135	228.859	950.0393	630.6102	210.0277	534.3281823	
	Skewness	30.8881954	-0.42748	-0.35963	27.45331	22.97042	-0.36175	13.36051178	
	std deviation	2.37141E+39	1.011297	1.012092	0.714537	7.953983	1.034084	3.95235E+38	2.3452
9	Variance	5.75E+78	1.675233	1.673196	0.529144	40.62386	1.753452	9.58425E+77	9.2510
	Kurtosis	956.91941	342.3227	342.8861	865.6727	448.2004	312.1299	544.688527	
	Skewness	30.888196	-10.9061	-10.5983	25.62825	15.94458	-10.1627	6.7989903	
	std deviation	2.39803E+39	1.294308	1.293521	0.727423	6.373685	1.32418	3.99672E+38	2.2026
10	Variance	1.92E+78	1.320847	1.331125	8.444569	59.5422	1.355039	3.20317E+77	14.3988
	Kurtosis	956.919239	407.9123	401.455	1526.454	132.1486	388.0901	635.4965805	
	Skewness	30.8881939	17.26229	16.63389	38.74158	5.623176	16.62999	20.96318625	
	std deviation	1.38633E+39	1.149281	1.153744	2.905954	7.716359	1.164061	2.31054E+38	2.8179

*For a description on the economic weighting sets please refer to Table 3.1.

PP = Partial pivoting in Delphi Matgen; FP = Full pivoting in Delphi Matgen; SVD = singular value decomposition in Delphi Matgen;
RIDGE = Adapted ridge regression in Delphi Matgen; Low PP = Partial pivoting in Clipper Matgen; Low FP = Full pivoting in Clipper Matgen

Table A 13 Spearman rank correlation coefficients for the different techniques in the forward prediction runs of the F_1 *P. patula* trials.

	Single traits			Economic weighting*									
Methods	**DBH**	**Stem form**	**Height**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
PP–FP	1.000	1.000	0.997	0.621	0.640	0.614	0.604	0.650	0.658	0.633	0.643	0.660	0.668
PP–SVD	1.000	1.000	0.997	0.551	0.543	0.537	0.522	0.542	0.572	0.562	0.546	0.552	0.572
PP–RIDGE				0.587	0.575	0.582	0.569	0.585	0.591	0.584	0.582	0.593	0.595
PP–Low PP	0.963	0.963	0.951	0.479	0.483	0.490	0.468	0.480	0.540	0.507	0.491	0.497	0.551
PP–Low FP	0.967	0.970	0.953	0.572	0.599	0.565	0.554	0.608	0.602	0.583	0.603	0.618	0.607
FP–SVD	1.000	1.000	1.000	0.871	0.831	0.835	0.824	0.814	0.807	0.866	0.828	0.815	0.783
FP–RIDGE				0.863	0.853	0.844	0.837	0.848	0.837	0.862	0.851	0.848	0.820
FP–Low PP	0.963	0.964	0.949	0.714	0.699	0.711	0.699	0.706	0.738	0.736	0.708	0.716	0.741
FP–Low FP	0.967	0.971	0.955	0.906	0.907	0.901	0.898	0.903	0.891	0.905	0.908	0.902	0.886
SVD–RIDGE				0.885	0.856	0.858	0.854	0.846	0.859	0.876	0.850	0.846	0.855
SVD–Low PP	0.963	0.964	0.949	0.649	0.607	0.618	0.600	0.603	0.623	0.658	0.617	0.614	0.604
SVD–Low FP	0.968	0.971	0.955	0.814	0.772	0.781	0.773	0.754	0.775	0.808	0.767	0.755	0.770
RIDGE–Low PP				0.615	0.614	0.607	0.598	0.618	0.641	0.631	0.621	0.627	0.637
RIDGE–Low FP				0.800	0.788	0.785	0.782	0.778	0.767	0.794	0.784	0.778	0.760
Low PP–Low FP	0.998	0.994	0.992	0.707	0.704	0.714	0.704	0.709	0.710	0.728	0.712	0.720	0.705

Correlation coefficient significant effect: All rank correlations significant $p<0.0001$

PP = Partial pivoting in Delphi Matgen; FP = Full pivoting in Delphi Matgen

SVD = singular value decomposition in Delphi Matgen; RIDGE = Adapted ridge regression in Delphi Matgen

Low PP = Partial pivoting in Clipper Matgen; Low FP = Full pivoting in Clipper Matgen

*For a description on the economic weighting sets please refer to Table 3.1

Table A 14 Realised genetic gains in standard deviation units for the F_1F_2 scenarios of *P. patula* trials.

Economic weighting*	Method											
	Partial pivoting		Full pivoting		SVD		Ridge regression		Low Partial pivoting		Low Full pivoting	
	T 10 %	B 10%	T 10 %	B 10%	T 10 %	B 10%	T 10 %	B 10%	T 10 %	B 10%	T 10 %	B 10%
1	-0.0863	-0.0087	0.0044	0.1037	0.0044	0.1037	-0.0153	0.0765	-0.1075	-0.1744	0.0044	-0.2405
2	-0.0777	0.0234	0.1824	-0.1231	-0.0405	-0.1046	0.0317	0.2120	0.0051	-0.1462	0.1796	-0.1524
3	-0.0785	-0.0335	-0.0300	-0.0495	-0.0318	-0.0684	0.0042	0.0575	-0.0019	-0.1432	-0.0300	-0.1396
4	-0.0756	-0.0164	-0.0166	-0.0509	-0.0206	0.0103	0.0271	0.1990	0.0017	-0.1311	0.1884	-0.1421
5	-0.0747	0.0534	0.2921	-0.0910	0.0742	-0.0811	0.0644	0.3196	0.2596	-0.3914	0.3056	-0.1163
6	-0.0892	-0.0238	-0.0648	-0.3631	-0.0068	-0.2620	-0.0805	-0.2067	0.0408	-0.2432	0.0437	-0.3631
7	-0.0919	0.0127	-0.0459	0.0167	0.0298	-0.0303	0.0285	0.0169	-0.0880	-0.1986	0.0473	-0.1486
8	-0.0783	0.0367	0.1813	-0.1109	-0.0471	-0.1012	0.0307	0.2164	0.2312	-0.1512	0.0396	-0.1400
9	-0.0783	-0.0887	0.2645	-0.0497	0.0738	-0.1012	0.0631	0.2744	0.2312	-0.3183	0.2599	-0.1400
10	-0.0788	-0.0553	-0.0273	-0.4003	0.0229	-0.2817	-0.1251	-0.2817	-0.0072	-0.2419	0.0913	-0.4712

T 10% = Realised genetic gains for the Top 10%
B 10% = Realised genetic gains for the bottom 10%
Low = low precision in Clipper Matgen
*For a description on the economic weighting sets please refer to Table 3.1.