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# Evaluation of an international series of *Pinus kesiya* provenance trials for adaptive, growth and wood quality traits

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By João Costa e Silva



**Title**

Evaluation of an international series of *Pinus kesiya* provenance trials for adaptive, growth and wood quality traits

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## Preface

An international series of provenance trials of *Pinus kesiya* was initiated by the IUFRO Working Party on Breeding Tropical Trees in 1984, and supported by the FAO Panel of Experts on Forest Gene Resources in 1988.

Searching for provenance locations and collection of seed for the establishment of field trials took place in the late 1980s in collaboration between national institutions in Brazil, Myanmar, China, Madagascar, Philippines, Thailand, Vietnam, Zambia, Zimbabwe, and the Oxford Forestry Institute and Danida Forest Seed Centre.

During 1989-1993, seed of 42 provenances and landraces from the nine countries mentioned above was distributed to 20 institutions in 19 countries. Thirty field trials were then established in 17 countries. In 1996, it was agreed to undertake a joint evaluation of a subset of these trials. During 1998-1999, a number of trials were assessed by national institutions in the respective countries, with technical and financial support from Danida Forest Seed Centre. Assessment reports were prepared for each of these trials. The reports and more information about the trial series can be found at the website of *Forest & Landscape*.

The present study involves an across-site analysis of some of the provenance trials. The interpretation of provenance performance across sites is often a complicated matter, due to the unbalanced representation of provenances amongst trials, as well as trait variance heterogeneity associated with differences between trials in measurement age and environmental variability. To accommodate these complexities, the analysis applied linear mixed model methodology, using a factor analytic structure to model the provenance effects across trials and a first-order separable autoregressive error term to model the residual variation in each trial. Such an approach is not commonly seen in the analysis of provenance trials, and the methods are therefore described in some detail with the intention that it might be useful to other researchers working with similar problems. The study was pursued by João Costa e Silva at *Forest & Landscape* during July-December 2006, with financial support from the *Danish Rectors' Conference* and the *Gabinete de Relações Internacionais da Ciência e do Ensino Superior* of Portugal.



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## **Abstract**

This study presents the results from seven international provenance trials of *Pinus kesiya* established in Colombia, South Africa, Swaziland, Vietnam and Zimbabwe. The traits evaluated were survival, total volume per hectare, Pilodyn penetration, stem straightness, branch diameter, forking and foxtailing, at ages 5, 6, 7 or 8 years from planting. The tested material included 28 seedlots, comprising 24 provenances from the natural range of the species distribution and 4 local seed sources from Madagascar and Zambia. Survival was generally high, with percentages exceeding 85% in most of the trials. Significant provenance variance was found for total volume per hectare, Pilodyn penetration, stem straightness, branch diameter and foxtailing in all of the trials where these traits were measured. Forking exhibited significant provenance variance in only four of the seven trials measured. A factor analytic structure, used to model the provenance effects in each trial indicated a strong provenance by environment (G x E) interaction for Pilodyn. However, the measurement age of Pilodyn differed between trials, and thus the detected G x E interaction may reflect differences between provenances in the radial age trend of wood density within the juvenile core. The practical importance of G x E interaction was not great for the other traits, as the majority of the provenances did not display relevant ranking changes across environments. Bivariate linear mixed model analyses across sites indicated that provenance correlations involving total volume per hectare, stem straightness and forking were statistically significant, moderate to high, and their signs suggested that simultaneous improvement could be achieved in these traits following provenance selection. However, these traits were significantly and adversely correlated with foxtailing. Provenance correlations involving Pilodyn and branch diameter were generally small and not significantly different from zero. Vietnamese provenances, as well as local seed sources from Madagascar and Zambia, provided favourable combinations of growth and wood quality traits, and thus could have an important value for provenance research, seed supply and breeding.

## **Keywords**

*Pinus kesiya*, provenance variation, genotype by environment (G x E) interaction, trait correlations, linear mixed models.

## Introduction

*Pinus kesiya* is a conifer species with an important potential for afforestation programmes in the tropical zone. The *P. kesiya* complex is widely distributed between 30°N and 12°N in South East Asia. It occurs in Burma, China, India, Laos, Philippines, Thailand, Tibet and Vietnam. The species grows best in medium to high rainfall conditions at medium altitudes (i.e. 600 to 1800 m). *P. kesiya* has the capacity to adapt to various environmental conditions. Provided that drainage is good, *P. kesiya* is adaptable to a broad range of soil types, tolerating nutrient poor and acid to neutral soils. In addition, it can withstand drought and frost. Nevertheless, at lower altitudes, *Pinus caribaea* and *Pinus oocarpa* are preferred, while at higher altitudes better results are obtained by various sub-tropical pines (e.g. *Pinus patula*) which are less frost sensitive (Armitage and Burley, 1980). Reporting on the mean annual volume increment of *P. kesiya* plantations, Varmola and Del Lungo (2003) indicated an average productivity of 19 m<sup>3</sup> ha<sup>-1</sup> year<sup>-1</sup> (range from 11 to 21 m<sup>3</sup> ha<sup>-1</sup> year<sup>-1</sup>, based on 59 observations) for an average rotation age of 20 years. The total plantation area of *P. kesiya* is not well known, but Vietnam alone accounts for around 250.000 ha (James and Del Lungo, 2005).

*P. kesiya* is a fast growing species and produces a high quality, long-fibered, pulp. However, poor stem form and branching characteristics have restricted the use of *P. kesiya* as a plantation species (Armitage and Burley, 1980). Stem defects such as basal sweep, butt sweep, sinuosity, crookedness, nodal swelling and multiple stems commonly occur, as do whorls of heavy persistent branches and long internodes (Burley and Wood, 1976). In addition, as for other fast growing tropical and sub-tropical pines, *P. kesiya* has a large juvenile core with less desirable wood properties such as lower density and short tracheid length. On favourable sites, promoting fast growth may also result in total tree collapse (Armitage and Burley, 1980). Therefore, opportunities to achieve genetic progress are substantial for traits with economic impact on plantation programmes using this conifer species in the tropical zone.

Initial research on inter-population differences in *P. kesiya* was pursued in Zambia during the 1950's. The test material included provenances from Assam (a State of



India), Philippines and Vietnam (Armitage and Burley, 1980). In 1969, the Food and Agricultural Organization (FAO) of the United Nations and the Australian Forest Research Institute sponsored seed collections of 19 seed sources of *P. kesiya* from the Philippines, which were complemented with two Zambian land races. Provenance trials were then established in several countries (Burley and Wood, 1976) but, when reviewing results from these trials, Gibson and Barnes (1984) recommended that a more comprehensive evaluation and analysis of the genetic variation in *P. kesiya* should be undertaken. Following these recommendations, and similar suggestions from the FAO Panel of Experts on Forest Gene Resources (FAO, 1988), a large collection of *P. kesiya* seed sources was carried out during the late 1980's, as a result of a collaborative effort between national institutions in different countries, including the Oxford Forestry Institute and Danida Forest Seed Centre (DFSC). In this context, during 1989-93, seed from provenances and land races of Burma, China, Madagascar, Philippines, Thailand, Vietnam and Zambia were distributed to several institutions in different countries. Although field experiments were initially planted in more countries, only trials established in Colombia, Indonesia, South Africa, Swaziland, Vietnam and Zimbabwe had high survival and were generally in good condition, as reported by DFSC (1996, 1997). For the remaining trials, either information was not received from the respective countries or the trials were abandoned due to severe damage caused by fire, drought or browsing.

Based on trial condition, as well as on the representation and distribution of provenances within and amongst trials, seven field experiments were considered in the present study to have relevant information for pursuing an across-site analysis of the *P. kesiya* international series mentioned above, and for traits with economic and biological importance. In this sense, the present work aims to: 1) assess the magnitude and significance of provenance variance and covariance in adaptive, growth and wood quality traits; 2) detect and determine the level of provenance by environment (G x E) interaction for the traits involved, as well as identify contrasting environments in terms of changes in provenance ranking; 3) evaluate the performance of different provenances across a range of environmental conditions, in order to be able to provide

recommendations concerning appropriate choices of seed sources for *P. kesiya* planting programmes in the tropics.

## **Materials and Methods**

### ***Genetic material, field trials and characters assessed***

Table 1 describes the location, climate and data information for each of the *P. kesiya* provenance trials of the international series used in the present study. The field trials were established in five different countries - Colombia, South Africa, Swaziland, Vietnam and Zimbabwe. Except for the trials in Colombia, the experimental sites were characterized for their soil physical and chemical properties, as described by Hansen *et al.* (2003). In this sense, all sites had acid (i.e. pH  $\approx$  5) and well drained soils with a medium/loamy texture; the organic matter content was poor (< 2% DM) in trials 2, 4 and 5, medium (2-5% DM) in trial 3, and rich (> 5% DM) in trial 1; soil depth was < 50 cm in trial 3, between 50 and 100 cm in trials 1, 4 and 5, and > 100 cm in trial 2. All trial sites are located outside the range of the natural distribution of *P. kesiya*. This also includes trial 1, as in northern Vietnam *P. kesiya* has a restricted distribution, being found in very small stands at elevations 650 - 850 m across the river Song Koi (Red) River in the vicinities of Lao Cai and Huang Su Phi (22°40'N, 104°35'E) (Armitage and Burley, 1980).

The present study included 28 *P. kesiya* provenances (see Appendix 1 for their definition, and description of the location and climate of their origin site). Most of the seedlots derive from collections made within the range of the natural distribution (i.e. in native stand localities) of the species. The exceptions are the Madagascar and Zambian provenances, which represent local seed sources. The Madagascar sources 25 and 26 are of Vietnamese origin, and derive from high quality stands managed for producing improved seed. The other Madagascar seedlot (provenance 27) presumably also originates from Vietnam, and was obtained from collections made within a land race. Provenance 28 pertains to a seed collection from ten trees of a clonal seed

orchard (CSO) in Zambia. Thus, the seedlots 25, 26 and 28 are likely to be improved by artificial selection, although no information is available concerning the traits targeted and the levels of improvement achieved. The representation and distribution of the sources within and across trials was unbalanced (see Appendix 1 for the list of trials where each provenance was tested): the number of provenances in each trial varied from 16 to 22, and the number of overlapping seedlots across trials varied from 8 to 19, with Trial 1 having the poorest provenance links (i.e. range from 8 to 12) with the other trials (Table 2). Nevertheless, the majority of the provenances were tested in at least four sites. In addition to plots with the targeted provenances, the trials also included plots with control seedlots from *P. kesiya*, as well as from other pine species (*Pinus elliottii*, *Pinus maximinoi*, *Pinus patula*, *Pinus taeda*, *Pinus tecunumanii* and *Pinus yunnanensis*). These controls had a sparse distribution across trials (i.e. not every control seedlot of every pine species occurred in each trial), and their representation within trials was smaller than the targeted provenances.

Except for the two trials established in Swaziland, the experimental layout was a randomised complete block design, although the design features differed amongst trials: the number of replicates varied from 4 to 6, and the size of the provenance plots within replicates ranged from 6 to 25 trees. In the Swaziland trials, the experimental layout was a triple lattice design, with 3 replicates, 5 incomplete blocks per replicate and 49 trees per provenance plot. Tree spacing was 2 m x 3 m for trial 1, 2.4 m x 2.4 m for trial 3, 2.7 m x 2.7 m for trials 2, 4 and 5, and 2.8 m x 2.8 m for trials 6 and 7. A coordinate system identifying individual tree positions was available for some trials only. Yet, plot positions could be assigned to a coordinate system in all trials, enabling the application of spatial analysis methods (see below) to model site variability by using plots as experimental units. In this sense, each trial was provided with a grid of  $c$  columns by  $r$  rows, and irregularly shaped trials were dealt with by expanding the data with the insertion of missing values.

As shown in Table 1, the field assessments occurred when the trees were 5 (trial 1), 6 (trial 2), 7 (trial 3) or 8 (trials 4 to 7) years from planting. Survival was recorded as alive or dead tree. Tree growth was evaluated by calculating the total over-bark tree volume using the function

$$V = 0.007118 + 0.00003603 \text{ DBH}^2 \text{ HT} \quad (1)$$

where  $V$  is the total individual tree volume (in  $\text{m}^3$ ),  $\text{DBH}$  is the breast-height diameter (in cm) and  $\text{HT}$  is the tree height (in m) (Sharma and Jain, 1977). Subsequently, total tree volume per hectare (VHA) was calculated for each plot as

$$\text{VHA} = [(\bar{V}/\text{Sp}) 10000] \text{ SUR} \quad (2)$$

where  $\bar{V}$  is the plot average of individual tree volumes,  $\text{Sp}$  is the tree spacing (in  $\text{m}^2$ ) and  $\text{SUR}$  is tree survival (i.e. the proportion of alive trees in the plot). Thus, this measure of volume production integrates both height and diameter growth, while accommodating differences between plots in survival. The wood quality traits included wood density (indirectly assessed in each tree by Pilodyn readings taken in a random aspect at breast-height), stem straightness (evaluated according to a 9-point scoring scale, where 1 and 9 indicate very crooked and straight stems, respectively), branch diameter (measured as the diameter of the largest branch in the whorl located at 1/10 of the tree height), forking (assessed as the presence or absence of one or more forks in the tree) and foxtailing (measured as the presence or absence of a foxtail in the tree). As in the case of volume production, observations on a plot basis were also obtained for the other traits (i.e. percentages of survival, forking and foxtailing, as well as plot means for Pilodyn penetration, stem straightness and branch diameter). All trials were assessed for survival, growth and forking, whereas measures of the remaining traits were available for some trials only (see the Results and Discussion section). Further details concerning the characters evaluated and the methods used in their measurement are described by Hansen *et al.* (2003). C. P. Hansen *et al.* (DFSC 2003) have reported single-trial results at <http://en.sl.life.ku.dk/dfsc/pdf/Kesiya%20Trials/PKT/index.html>, where further details on the various trials and their history can also be found.

## *Data analysis*

Plots were used as experimental units in the data analysis for all traits. Some diagnostics (i.e. Shapiro-Wilk test, Jarque-Bera statistic and quantile-quantile plots) indicated that the data deviated from a normal distribution for survival and foxtailing. An arcsine transformation (i.e.  $\sin^{-1}(\sqrt{y})$ , where  $y$  is the proportion of alive trees, or the proportion of trees with foxtails, in a plot) improved the normality, and so all the analyses of these two traits were pursued on the basis of transformed plot observations.

The variance parameters, under the general linear mixed model described below, were estimated by restricted maximum likelihood (REML, Patterson and Thompson, 1971), using the average information (AI) REML algorithm (Gilmour *et al.*, 1995). Standard errors were also calculated for some parameter estimates, according to the general expression for the variance of a ratio, based on an approximation using Taylor series expansion (Lynch and Walsh, 1998). In the context of the statistical hypothesis tests carried out in the present work, the designations “significant” and “not significant” refer to significance probabilities  $P \leq 0.05$  and  $P > 0.05$ , respectively. ASREML (Gilmour *et al.*, 2006) and SAS (SAS Institute Inc., 2004) were the statistical programs used in the data analysis.

### *Analysis of individual traits*

Across-site analyses of individual traits were undertaken within the framework of the general linear mixed model:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_0\mathbf{u}_0 + \mathbf{Z}_g\mathbf{u}_g + \mathbf{e} \quad (3)$$

where  $\mathbf{y}$  is the  $N \times 1$  combined vector of plot observations across trials for a given trait ( $N = \sum_{i=1}^p N_i$ , where  $N_i$  is the number of plots in the  $i^{th}$  trial,  $i = 1 \dots p$ ),  $\mathbf{b}$  is the  $t \times 1$  vector of fixed effects with a  $N \times t$  incidence matrix  $\mathbf{X}$ ,  $\mathbf{u}_g$  is the  $np \times 1$  vector for the random effects of  $n$  ( $n = 1 \dots 28$ ) provenances in each of  $p$  trials with a  $N \times np$  incidence matrix  $\mathbf{Z}_g$ ,  $\mathbf{u}_0$  is the  $m \times 1$  vector of additional random effects with a  $N \times m$

incidence matrix  $\mathbf{Z}_0$ , and  $\mathbf{e}$  is the  $N \times 1$  vector of residual terms (i.e. the plot error effects in each of  $p$  trials).  $\mathbf{Z}_g$  contained some columns of zeros, as not all the provenances were tested in all trials. Thus, the unbalanced nature of the data was handled and (through the variance-covariance structure of  $\mathbf{u}_g$ , see below) predictions of performance were obtained for every provenance in each trial. However, for a given trait, the accuracy of these predictions will be higher for provenances having data available in more trial sites.

The vector  $\mathbf{u}_0$  had sub-vectors of random effects for replicates, incomplete blocks within replicates (i.e. trials 4 and 5), and a term to fit the variation between seedlots within the control material for each trial. The terms in  $\mathbf{b}$  comprised the overall mean, trial main effects and trial specific effects. The latter included a factor with two levels to account for mean differences between the group of targeted *P. kesiya* provenances in  $\mathbf{u}_g$  and the group of control seedlots in  $\mathbf{u}_0$  for each trial. Although the control seedlots are not the main focus of the present study, their data was retained in the analysis so that all the observations could be used when applying a spatial correlation model to accommodate the residual variation within trials.

Under the linear mixed model defined in (3), the joint distribution of the random terms was assumed to be multivariate normal, with the mean vector and variance matrix defined as:

$$\begin{bmatrix} \mathbf{u}_0 \\ \mathbf{u}_g \\ \mathbf{e} \end{bmatrix} \sim N \left( \begin{bmatrix} \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \begin{bmatrix} \mathbf{G}_0 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{G}_g & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{R} \end{bmatrix} \right) \quad (4)$$

where  $\mathbf{G}_0$ ,  $\mathbf{G}_g$  and  $\mathbf{R}$  are variance matrices pertaining to  $\mathbf{u}_0$ ,  $\mathbf{u}_g$  and  $\mathbf{e}$ , respectively.

Separate model terms in  $\mathbf{u}_0$  were assumed to be mutually independent, and thus  $\mathbf{G}_0$  was defined as  $\bigoplus_{j=1}^q \mathbf{G}_{0_j}$ , where  $\mathbf{G}_{0_j}$  is the variance matrix for the  $j^{\text{th}}$  random term ( $j = 1 \dots q$ ), and  $\bigoplus$  is the direct sum operation. In addition, for the  $j^{\text{th}}$  random term in  $\mathbf{u}_0$ , the effects were assumed to be independent across trials, and thus  $\mathbf{G}_{0_j} = \bigoplus_{i=1}^p \sigma_{j_i}^2 \mathbf{I}_{n_j}$ ,

where  $\sigma_{j_i}^2$  is the variance parameter associated with the  $j^{th}$  term in the  $i^{th}$  trial and  $\mathbf{I}_{n_j}$  is an identity matrix of dimension  $n_j \times n_j$  ( $n_j =$  number of levels of the  $j^{th}$  term).

Therefore, heterogeneity of variance was allowed between trials for effects in  $\mathbf{u}_0$ .

The plot error effects from different trials were assumed to be independent, leading to  $\mathbf{R} = \bigoplus_{i=1}^p \mathbf{R}_i$ , where  $\mathbf{R}_i$  is the variance matrix for the residual terms in the  $i^{th}$  trial. As a preliminary step, spatial analysis was pursued for each trial, and ignoring the across-site relationships for effects in  $\mathbf{u}_g$ . This was necessary in order to determine the adequate model to be subsequently incorporated in  $\mathbf{R}_i$  for the across-site analysis. Spatial analysis allows  $\mathbf{R}_i$  to include a correlation structure. Previous studies with agricultural varieties (Gilmour *et al.*, 1997; Cullis *et al.*, 1998) and forest tree species (Costa e Silva *et al.*, 2001; Dutkowski *et al.*, 2002) have shown that a separable autoregressive process of order 1 (AR1) is usually a reasonable variance structure for modelling the residual variation within field trials. In this sense,  $\mathbf{R}_i$  was defined as:

$$\mathbf{R}_i = VAR(\xi_i) = \sigma_{\xi_i}^2 [\sum_{c_i}(\phi_{c_i}) \otimes \sum_{r_i}(\phi_{r_i})] \quad (5)$$

where  $\xi_i$  represents the spatially correlated residual term,  $\sigma_{\xi_i}^2$  is the variance of the trend process,  $\sum_{c_i}$  and  $\sum_{r_i}$  are first-order autoregressive correlation matrices with autocorrelation parameters  $\phi_{c_i}$  and  $\phi_{r_i}$  for the columns and rows (respectively) of the  $i^{th}$  trial, and  $\otimes$  is the Kronecker product. Model (5) allows for heterogeneous residual variances between trials, and a separate spatial correlation structure for the plot errors in each trial. Based on the method of Gilmour *et al.* (1997), sample variograms and plots of spatial residuals were used as diagnostic tools for identifying and modelling additional sources of environmental variability, and thus to extend the initial model in (5). Following this approach, trial specific terms were included in  $\mathbf{b}$  and/or  $\mathbf{u}_0$  (as appropriate) to fit global trend and/or extraneous variation aligned with design factors (such as columns and/or rows). In few cases (i.e. particularly in trials where the spatial correlation was strong for the analysed trait), a spatial uncorrelated residual term  $\eta_i$

could also be estimated, and  $VAR(\boldsymbol{\eta}_i)$  (equal to  $\sigma_{\eta_i}^2 \mathbf{I}_{N_i}$ , where  $\sigma_{\eta_i}^2$  is the variance of the uncorrelated residuals and  $\mathbf{I}_{N_i}$  is an identity matrix of dimension  $N_i \times N_i$ ) was added to  $VAR(\boldsymbol{\xi}_i)$  in (5). In the spatial modelling process, the design features (i.e. replicates and incomplete blocks) were kept in the mixed linear model irrespective of whether or not they were significant, in order to reflect the original randomization process. In this sense, the spatial approach is not a substitute for the randomization-based model, but an additional tool which recognizes that residual variation may not be all spatially independent, and thus uses an error variance model to accommodate the actual patterns of site variation. When retaining the design features, it may be necessary to allow the respective variances to be negative, as discussed by Nelder (1954). However, in some cases, this has impaired convergence in the mixed model analysis, and consequently the design features in question were dropped from the model or their variances were constrained to be positive. Two-tailed likelihood ratio (LR) tests were pursued in the final extended model to test whether the estimated autocorrelation parameters deviated significantly from zero, and then significant parameters were retained in  $\mathbf{R}_i$ . When both  $\phi_{e_i}$  and  $\phi_{r_i}$  were found to be small and not significant, the residuals in  $\mathbf{R}_i$  were assumed to be independent, and thus  $\mathbf{R}_i$  was defined as  $\sigma_{e_i}^2 \mathbf{I}_{N_i}$ , where  $\sigma_{e_i}^2$  is the plot error variance.

After determining the appropriate model for the plot errors, and still ignoring the across-site relationships for effects in  $\mathbf{u}_g$ , the statistical significance of the provenance variance was assessed for each trial via one-tailed LR tests. In addition, the average accuracy of best linear unbiased predictors (BLUPs) of provenance effects in  $\mathbf{u}_g$  was calculated from:

$$\hat{r}_{g\hat{g}_i} = \sqrt{1 - \frac{PEV_i}{\hat{\sigma}_{g_i}^2}} \quad (6)$$

where  $\hat{\sigma}_{g_i}^2$  and  $PEV_i$  are variance estimates for provenance and average prediction error (respectively) in the  $i^{th}$  trial.  $\hat{r}_{g\hat{g}_i}$  measures the average correlation between the



predicted and true genetic effects (Falconer and Mackay, 1996), and the reliability  $\hat{r}_{gg_i}^2$  was used to express the accuracy of provenance selection for a given trait in each specific trial.

Theoretically, an unstructured (US) form of  $\mathbf{G}_g$  would be the most complete variance model to fit the effects for  $n$  provenances in each of  $p$  trials. However, the number of parameters to be estimated in the US matrix is  $p(p+1)/2$ , and so the estimation process may become unstable as  $p$  increases due to an over-parameterized model (Smith *et al.*, 2001; Thompson *et al.*, 2003; Costa e Silva *et al.*, 2006). Indeed, the across-site analysis of two of the traits evaluated in this study could not converge when the US matrix was used. Therefore, for the across-site analysis of all traits, a more parsimonious approach was pursued to fit the effects in  $\mathbf{u}_g$  and, thereby, a multiplicative model associated with factor analysis was applied as an approximation to the US form. In this sense, the provenance effects in each trial were modelled as:

$$\mathbf{u}_g = (\mathbf{\Lambda} \otimes \mathbf{I}_n) \mathbf{f} + \boldsymbol{\delta} \quad (7)$$

with  $\mathbf{f}$  and  $\boldsymbol{\delta}$  assumed to be independent normal variables with zero means and variance matrices  $VAR(\mathbf{f}) = \mathbf{I}_{nk}$  and  $VAR(\boldsymbol{\delta}) = \boldsymbol{\Psi} \otimes \mathbf{I}_n$  (respectively), leading to a variance matrix  $\mathbf{G}_g$  of the form:

$$\mathbf{G}_g = (\mathbf{\Lambda} \mathbf{\Lambda}' + \boldsymbol{\Psi}) \otimes \mathbf{I}_n \quad (8)$$

where  $\mathbf{\Lambda}$  is a  $p \times k$  matrix of loadings ( $k$  = number of fitted factors),  $\mathbf{f}$  is a  $nk \times 1$  vector of scores,  $\boldsymbol{\delta}$  is a  $np \times 1$  vector of lack of fit terms for the multiplicative model,  $\boldsymbol{\Psi}$  is a  $p \times p$  diagonal matrix of “specific” (lack of fit) variances for individual trials,  $\mathbf{I}_{nk}$  and  $\mathbf{I}_n$  are identity matrices, and  $'$  denotes matrix transpose. Model (7) is a multiplicative model of environment and provenance coefficients, being regarded as a regression of the provenance effects  $\mathbf{u}_g$  on (unknown) environmental covariates  $\mathbf{\Lambda}$  with different (random) regression coefficients  $\mathbf{f}$  for each provenance. For a given provenance, the regression coefficient in  $\mathbf{f}$  can be considered as a measure of the sensitivity of trait

response to the environmental covariates. The  $\mathbf{G}_g$  matrix described in (8) is known as factor analytic (FA) structure of order  $k$  (Mardia *et al.*, 1988). As in the US form of  $\mathbf{G}_g$ , the FA structure allows for heterogeneous provenance variances and correlations between trials. The provenance variance for the  $i^{th}$  trial is estimated by  $\sum_{l=1}^k \lambda_{li}^2 + \Psi_i$ , where  $\lambda_{li}$  and  $\Psi_i$  are, respectively, the loading for the  $l^{th}$  factor ( $l = 1 \dots k$ ) and the specific variance in the  $i^{th}$  trial. The across-site correlation matrix ( $\mathbf{C}$ ) for effects in  $\mathbf{u}_g$  is calculated by  $\mathbf{C} = \mathbf{\Lambda}^{(c)} \mathbf{\Lambda}^{(c)'} + \mathbf{\Psi}^{(c)}$ , where  $\mathbf{\Lambda}^{(c)} = \mathbf{D}^{-1} \mathbf{\Lambda}$  and  $\mathbf{\Psi}^{(c)} = \mathbf{D}^{-2} \mathbf{\Psi}$  are the matrices of loadings and specific variances (respectively) on a correlation scale, and  $\mathbf{D}$  is a  $p \times p$  diagonal matrix of provenance standard deviations. Under a restricted form of a FA model with one factor (i.e. FA(1)), all the across-site correlations were constrained to be equal to one. This restricted model was then compared to an unconstrained model allowing the across-site correlations to be different, in order to test the statistical significance of the G x E interaction for provenance effects using a one-tailed LR test. When  $k > 1$ , the FA structure is not unique under rotation (Mardia *et al.*, 1988) and, thereby, constraints were imposed on the elements of  $\mathbf{\Lambda}$  for parameter identifiability (Smith *et al.*, 2001). Moreover, the FA structure may have less than full rank if some elements in  $\mathbf{\Psi}$  are constrained to remain within the parameter space, which may lead to convergence problems. To accommodate this possibility, a modified AI algorithm for fitting reduced-rank models (Thompson *et al.*, 2003) was used. BLUPs of provenance effects were obtained for each trial after analysing simultaneously all data by using the FA structure for modelling the effects in  $\mathbf{u}_g$ . Generalized least-squares estimates of trial means were also obtained, based on the data provided by the group of targeted *P. kesiya* provenances.

### *Analysis of pairs of traits*

Bivariate analyses of pairs of traits were conducted by using simultaneously data from all trials with information, as well as significant provenance variance, for both traits. The aim was to obtain common estimates for within- and across-site correlations between traits for effects in  $\mathbf{u}_g$ . In this context, the variance matrix  $\mathbf{G}_g$  was defined by:

$$\left( \begin{bmatrix} \mathbf{D}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{D}_2 \end{bmatrix} \begin{bmatrix} \mathbf{C}_1 & \mathbf{C}_{1,2} \\ \mathbf{C}_{2,1} & \mathbf{C}_2 \end{bmatrix} \begin{bmatrix} \mathbf{D}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{D}_2 \end{bmatrix} \right) \otimes \mathbf{I}_n \quad (9)$$

where  $\mathbf{D}_1$  and  $\mathbf{D}_2$  are diagonal matrices of provenance standard deviations for traits  $I$  and 2 (respectively) in each trial,  $\mathbf{C}_1$  and  $\mathbf{C}_2$  are across-trial correlation matrices for a given trait, and  $\mathbf{C}_{I,2}$  ( $= \mathbf{C}'_{2,I}$ ) is a matrix with correlations between traits within (on the diagonal) and across (on the off-diagonal) trials. All the elements in  $\mathbf{C}_1$  and  $\mathbf{C}_2$  were constrained to remain fixed at constant values, which were specified on the basis of the pattern of correlations estimated from the previous across-site analysis of each trait. In this sense, the constraints were imposed as follows. If, for example, in trait  $I$  all the trials were all highly correlated, then the elements in  $\mathbf{C}_1$  were all fixed at an overall average correlation. Conversely, if there were contrasting clusters of highly correlated trials, then the elements in  $\mathbf{C}_1$  were fixed at average correlation values obtained within and across each group of trials. A similar procedure was adopted if the contrast was between single trials and groups of highly correlated trials. Two constraints were also imposed within  $\mathbf{C}_{I,2}$  to equalize its diagonal and off-diagonal elements, and thus to get common estimates for within- and across-site correlations amongst traits. Two-tailed LR tests were pursued to test whether the estimated common correlation amongst traits within trials was significantly different from that across trials. If the LR test indicated that these two correlation estimates were not significantly different, then all the elements in  $\mathbf{C}_{I,2}$  were constrained to be equal, and an overall correlation between traits was calculated. In a final step, two-tailed LR tests were also undertaken to test whether the estimated trait correlations deviated significantly from zero.

The bivariate analyses of pairs of traits retained all the terms that were included in  $\mathbf{b}$  and  $\mathbf{u}_0$  under the across-site analyses of individual traits. For terms in  $\mathbf{u}_0$ , the effects were again assumed to be independent across trials, and the trait covariances were ignored within trials. In particular, the number of replicates was not large and the incomplete block terms were generally not significant, which would not result in meaningful trait correlation estimates for these effects. The plot error effects from

different trials were also assumed to be independent, and  $\mathbf{R}_i$  was defined as  $\Sigma_{\xi_i} \otimes [\Sigma_{c_i}(\phi_{c_i}) \otimes \Sigma_{r_i}(\phi_{r_i})]$ , where  $\Sigma_{\xi_i}$  is a (2 x 2) trait variance-covariance matrix for the residual terms  $\xi_i$  in the  $i^{\text{th}}$  site. Under this definition of  $\mathbf{R}_i$ , the variances of the trend process are allowed to be heterogeneous between traits, but common  $\phi_{c_i}$  and  $\phi_{r_i}$  parameters are assumed for both traits. Two-tailed likelihood ratio (LR) tests were again pursued to test the deviation of the estimated autocorrelation parameters from zero, and then significant parameters were retained in  $\mathbf{R}_i$ .

## Results and discussion

Tables 3 to 8 present the results obtained for total volume per hectare (VHA), Pilodyn penetration (PIL), stem straightness (ST), branch diameter (BD), forking (FRK) and foxtailing (FOX), for the across-site analyses using the FA structure to model the provenance effects in  $\mathbf{u}_g$ . In these tables, for each trial  $i$ , parameter estimates are given for the generalised least-squares site mean, provenance variance (presented as both an absolute value  $\hat{\sigma}_{g_i}^2$ , and as a percentage of the trial mean, i.e. the coefficient of variation), factor loadings (given on the covariance,  $\hat{\lambda}_i$ , and correlation,  $\hat{\lambda}_i^c$ , scales), specific variance ( $\hat{\psi}_i$ ) and the percentage of variance explained by the regression part of the model (VE). For a subset of the provenances, Figures 1 and 2 depict graphically the G x E interaction for VHA and PIL, respectively. For each of the evaluated traits, Table 9 shows the BLUPs of provenance effects for single trials or averaged across trials, based on the patterns of G x E interaction revealed by the across-site analyses. Table 10 gives the estimates of provenance correlations between traits, provided by bivariate analyses.

## *Analysis of individual traits*

### *Survival*

Survival (SUR) was measured in all trials. As shown in Table 1, mean SUR was generally high for the *P. kesiya* sources in the international series, with percentages exceeding 85% in most of the trials. Trial 1 had a somewhat lower mean SUR than the others. Moreover, preliminary spatial analysis for each trial indicated that  $\hat{\sigma}_{g_i}^2$  was low and not significant for all trials except trial 4. For this trial,  $\hat{r}_{gg_i}^2$  was 0.62. Given these results, it was decided to estimate a pooled  $\hat{\sigma}_{g_i}^2$  in the across-site analysis, and assuming variance homogeneity for effects in  $\mathbf{u}_g$ . In addition, the effects in  $\mathbf{u}_g$  were assumed to be equally correlated between different trials. Based on the results from spatial analysis, the final model for the combined trial data retained significant AR1 parameters across rows and/or columns for two trials (with a  $\boldsymbol{\eta}_i$  term being included in one trial), as well as linear trends across rows and/or columns in  $\mathbf{b}$  for three trials, a spline term in  $\mathbf{u}_0$  for one trial and column effects in  $\mathbf{u}_0$  for one trial. Following this analysis, the common  $\hat{\sigma}_{g_i}^2$  was marginally significant (i.e.  $P = 0.02$ ) and the estimated common correlation across sites for provenance effects was close to one (not shown). The latter result suggested no G x E interaction for SUR, and led to similar BLUPs for the effects of a given provenance across different trials.

Sources from Burma, Madagascar and Zambia were amongst the poor performers for SUR (Table 9). There was no clear geographic pattern between the other sources, with seedlots 1 from the Philippines, 7 and 8 from Vietnam, 11, 14 and 15 from Thailand, and 21 from China, being amongst the 25% best. When expressed as percentages of the overall mean, the expected responses in SUR from selecting the provenances with the poorest (i.e. 24) and the best (i.e. 1) ranks were -4.2 and 2.3%, respectively (Table 9). These responses were not large, and may be considered unimportant given that the general level of SUR was high in the trials. In addition, the modest difference between the two extremes in expected response reflects the limited

ability to discriminate between the sampled provenances for SUR in the examined trial sites.

### *Total volume per hectare*

VHA was measured in all trials. Preliminary spatial analysis of VHA detected significant AR1 parameters across rows and/or columns for three trials (with a  $\eta_i$  term being included in one trial), as well as linear trends across rows and/or columns in  $\mathbf{b}$  for four trials, a spline term in  $\mathbf{u}_0$  for one trial and column effects in  $\mathbf{u}_0$  for three trials. Significant  $\hat{\sigma}_{g_i}^2$  were found for all trials. The  $\hat{r}_{gg_i}^2$  estimates ranged from 0.56 to 0.88 (mean = 0.73), with the lowest and the highest precision for discriminating between provenances being obtained for trials 5 and 2, respectively.

The analysis would not converge when an US form (with 28 parameters) was used in  $\mathbf{G}_g$ . Adding a second factor in the FA structure (i.e. FA(2), with 20 parameters) did not result in a significant improvement over a FA(1) model. As shown in Table 3, the average percentage of provenance variation explained by the regression implied in the FA(1) model was reasonable (i.e. 73%), with more than 70% of the provenance variance being accounted for by one factor in all trials except trial 1. Although there is some lack of fit in the model, the results suggested that the FA(1) structure was a plausible parsimonious approach (with 14 parameters) to provide an approximation to the US form. A FA(1) model constraining the correlations between trials to be all equal to one (hereafter called FA(1)\_C) had a substantially worse fit than a FA(1) structure where the correlations were allowed to be different (as in Table 3), which indicated that G x E interaction was statistically significant for effects in  $\mathbf{u}_g$ .

As shown in Table 3, trials 1 and 6 had the lowest and the highest site means for VHA, respectively. The same tendency was found for the magnitude of  $\hat{\sigma}_{g_i}^2$ , and the heterogeneity of these variance estimates was significant, as revealed by a two-tailed LR test. Although also representing ranking changes, the covariance loadings  $\hat{\lambda}_i$  were strongly positively associated with  $\hat{\sigma}_{g_i}^2$ , suggesting that the differences in provenance

variance may have had a major influence on  $\hat{\lambda}_i$ . Part of the heterogeneity in  $\hat{\sigma}_{g_i}^2$  reflects the direct relationship among means and variances due to trial differences in measurement ages and growth environment. However, the coefficients of provenance variation (CV) ranged between 8.5% and 19%, indicating that the trials also differed in the actual expression of provenance effects. In this sense, the largest levels of variation were observed in trials 3 and 6, which had also the highest values for  $\hat{\lambda}_i$ .

The correlation loadings  $\hat{\lambda}_i^c$  express mainly rank changes, and they indicated that trial sites other than 1 tended to have high pairwise provenance correlations (Table 3). Based on the FA(1) model parameters, the average of the across-site correlations between trial 1 and the others was 0.42, whereas the mean estimate obtained for all trials except trial 1 was 0.81. These results suggest a pattern of G x E interaction defined by a contrast of trial 1 with the group formed by the remaining trials. The change in ranking between trial 1 and the others is illustrated in Figure 1 where, for the vector of loadings (labelled by trial number) in  $\mathbf{\Lambda}$ , the fitted regression lines are depicted for a subset of the provenances (i.e. 8 and 23, which had the largest estimated absolute scores, and 13 and 15, where the values in  $\mathbf{f}$  were intermediate). Nevertheless, the pattern of provenance response to  $\hat{\lambda}_i$  seems to be dominated by alterations of scale associated with differences between trials in  $\hat{\sigma}_{g_i}^2$ . In this sense, the provenances gradually diverged as  $\hat{\lambda}_i$  increased, without shifts in ranking from trial 5.

As presented for VHA in Table 9, the seedlots from Burma, Madagascar and Zambia, as well as the majority of the Vietnamese and Chinese provenances, had usually small changes in ranking between trial 1 and their average performance in the other trials. On the other hand, the Thai provenances were generally less consistent in their rank. Major shifts in ranking also occurred for provenances 2 and 4 (Philippines), 8 (Vietnam) and 22 (China). The Burmese provenances had consistently the poorest growth while for trial sites other than 1, the Vietnamese seedlots were usually superior, and the Philippines sources tended to be intermediate. In addition, for these sites, seedlots 25 and 26 from Madagascar (which are also of Vietnamese origin), as well as the Zambian source 28, were good performers. As referred above, these three

seedlots are likely to have been improved to some extent, and thus their good performance for VHA may partly reflect the effect of previous selection for growth rate. Several provenance studies with growth traits in *P. kesiya* (Armitage and Burley, 1980, pages 47-54; Mullin *et al.*, 1984) have indicated a general inferiority of Burmese provenances, whereas Vietnamese seedlots tended to be superior or similar to sources from the Philippines. As for the Vietnamese source 8 in Figure 1, the seedlots that showed the best mean performance for trial sites other than 1 (Table 9) had also the largest estimated positive scores in **f**, which suggests that they were more sensitive to the environmental conditions implicit in the (unobservable) covariate in **A**.

As described by Armitage and Burley (1980, pages 90-95), *P. kesiya* grows best in areas with a distinct seasonal pattern of rainfall and an annual precipitation above 700 mm, relative humidity of 60% or more in the spring and up to 85% in the summer, and at altitudes from 600 to 1800 m (although it has displayed outstanding growth on some sites at higher elevations). In addition, the ideal temperature regime for *P. kesiya* is one with warm to hot summers (i.e. mean monthly temperatures up to around 25 °C in the hottest months) and cool to cold winters (i.e. mean monthly temperatures down to around 8 °C in the coldest months). These conditions pertain to the regions where the species grows naturally, as well as outside them in Asia, Africa and South America. Except for trial 1, where the conditions for elevation and temperature variables may be more extreme, the trial sites evaluated here tend to satisfy these requirements (Table 1). When comparing all the rainfall and temperature variables between the trial sites (Table 1) and the native stand localities (i.e. provenances 1 to 24, Appendix 1), the climatic observations in the provenance localities of Vietnam are within or close to the ranges of corresponding values in the trials. The other native stand localities tend to diverge more from the ranges of the trial sites in terms of precipitation (e.g. AP and PDM in the Philippines; PDM in Thailand) or temperature (e.g. MTWM in Thailand; MTCM in China and Burma) variables. In particular, the records for the precipitation variables in the Vietnamese native stands approach those in trial 6. Moreover, trial 6 had the highest value for the minimum monthly moisture availability index (Table 1). Dry season soil moisture supply is a relevant soil parameter for *P. kesiya* performance, as it sustains dry season diameter and height growth (Armitage and Burley, 1980).



These factors may have contributed to the greatest magnitude obtained for  $\hat{\sigma}_{g_i}^2$  in VHA at this trial.

Although rankings vary noticeably for some provenances, it may be concluded that the practical importance of G x E interaction for VHA seems to be small for the trials evaluated here, given that it was particularly driven by one outlying site and was dominated by changes in scale related to differences between trials in provenance variation. Several reasons can be pointed out as an attempt to explain the outlying behaviour of trial 1. The trial was measured earlier than the others, and so it is possible that provenance variation and performance may be altered with age. Mortality was higher in trial 1, and may have affected the expression of provenance variation at the site. In terms of genetic links, trial 1 had the poorest connections with other trials, which may have reduced the efficiency of estimation for provenance effects. Finally, when compared with the other trial sites, the combination of site features in trial 1 (Table 1) - namely a hot, humid, tropical area at lower elevations - may be less favourable for the growth of *P. kesiya* (Armitage and Burley, 1980).

#### *Wood density*

PIL was measured in trials 1 to 5. Previous spatial analysis of PIL revealed significant AR1 parameters across columns only and for four trials (with  $\eta_i$  terms being retained in two trials), and included linear trends across rows and/or columns in  $\mathbf{b}$  for two trials, as well as spline terms in  $\mathbf{u}_0$  for two trials. Significant  $\hat{\sigma}_{g_i}^2$  were detected for all trials. The  $\hat{r}_{gg_i}^2$  estimates ranged from 0.47 to 0.86 (mean = 0.67). The lowest and highest  $\hat{r}_{gg_i}^2$  estimates were obtained for trials 1 and 2, respectively; the remaining trials had more homogeneous  $\hat{r}_{gg_i}^2$  values, varying from 0.61 to 0.70.

Convergence could not be achieved when the analysis used an US form of  $\mathbf{G}_g$ . A FA(2) model with 14 parameters (i.e. one less than the US form) did not improve significantly the analysis over the FA(1) model. As shown in Table 4, the multiplicative part of the FA(1) model explained more than 90% of the provenance

variance in four trials and, on average, the percentage of variance accounted for was 81%. These results suggested that the FA(1) model was a reasonable parsimonious approximation (with 10 parameters) to the US form. Allowing the correlations across sites to be different in the FA(1) model provided a substantially better fit than a FA(1)\_C structure, and indicated that G x E interaction was statistically significant for effects in  $\mathbf{u}_g$ .

Trials 1 and 2 had the highest site means for PIL, suggesting a lower level of breast-height wood density at these trials (Table 4). However, these two trials were measured at a younger age than the others, and thus the differences in site means may reflect to some extent the influence of the age trend in wood density at breast height. Indeed, in *P. kesiya*, the pattern of within-tree radial variation in wood density is defined by a strong increase from the pith until about annual ring ten, from where it will gradually stabilize (Armitage and Burley, 1980). The magnitude of  $\hat{\sigma}_{g_i}^2$  was also higher in trials 1 and 2, but the estimates were not significantly different from each other, as indicated by a two-tailed LR test. In addition, the range of the CV estimates was small, which also suggests that the actual levels of provenance variation were similar between trials.

As indicated by the  $\hat{\lambda}_i^c$  estimates (Table 4), trials 3 to 5 were strongly positively correlated, weakly negatively correlated with trial 1, and strongly negatively correlated with trial 2. Trials 1 and 2 were positively correlated; however, the magnitudes of  $\hat{\lambda}_i^c$  differed considerably, indicating that the correlation between these trials was weak. The average correlation across all trials was close to zero (i.e. -0.06). The G x E interaction is displayed in Figure 2 for a subset of the provenances (i.e. 2, 11, 13 and 23, which had contrasting estimated scores in  $\mathbf{f}$ ). The fitted regression lines in Figure 2 depict a typical crossover interaction between the group of trials 3 to 5 and the other two trials. Thus, for PIL, the pattern of provenance response to  $\hat{\lambda}_i^c$  seems to be dominated by changes in ranking.

The contrasts between the provenance rankings in trials 1, 2 and the group of trials 3 to 5, are illustrated for PIL in Table 9. Although there were some changes in ranking (being particularly marked for seedlots 4, 6, 8, 9, 16, 22 and 24) between trials 1 and 2,

there was a general trend for the Philippines sources to have higher wood density in these trials, whereas the Thai seedlots had usually lower wood density. The group of trials 3 to 5 had an opposite pattern, with the seedlots from the Philippines having the lowest wood density, while the Thai, as well as Chinese sources, had the highest densities. When compared with their performance in trials 1 and 2, the seedlots from Madagascar and Zambia tended to have lower wood density in trials 3 to 5. Nevertheless, in trials 1 and 2, sources 25, 26 and 28 tended to have a similar behaviour in terms of ranking for both VHA and PIL, which may suggest that previous selection for growth did not affect wood density. There was no consistent pattern across sites for the Vietnamese sources, but generally they were intermediate in trials 3 to 5. Also in this group of trials, the Burmese sources showed a low level of wood density.

Following the evaluation of a series of *P. kesiya* trials in Zimbabwe, Mullin *et al.* (1984) reported a significant negative correlation between basic density determined at 6½ years and the altitude of provenance collection locality, and they interpreted this result as the effect of soil-moisture status on basic density. In this sense, sources from the lowlands had higher basic density, as they were adapted to a higher degree of dry-season soil moisture stress. As indicated by the moisture availability index values in Table 1, water deficit in the dry season may be somewhat milder in trials 1 and 2 than in trials 3 to 5. Thus, it is possible that some of the changes in ranking referred above could be the result of provenance adaptation to differences between trials in dry-season soil moisture stress. The Thai sources, for example, originate from localities where water deficit may be severe in the dry season (as suggested by the magnitudes of the moisture availability index in Appendix 1), and thus may have had a better ability for producing more dense wood in the group of trials 3 to 5. However, using this argument does not explain the behaviour of the other seedlots. In addition, the difference in measurement ages between the trials is likely to have an important impact on the G x E interaction for PIL. In this context, as the gradient of wood density from the pith towards the bark is greatest in the juvenile core of *P. kesiya* (which may extend to the inner ten annual rings, Armitage and Burley, 1980), it is probable that different provenances have different trends of radial variation with age, in which case the G x E

interaction reported here for PIL will be confounded by the presence of a provenance by time interaction in wood density. Although the PIL measures in trials 3 to 5 may be more reliable in terms of age, older assessments will be needed for PIL to provide a more efficient basis for seed source selection for wood density.

### *Stem straightness*

ST was measured in trials 1 to 5. Spatial analysis of ST found significant AR1 parameters across rows and/or columns for two trials, and identified linear trends across rows and/or columns in  $\mathbf{b}$  for four trials, while a spline term was used for  $\mathbf{u}_0$  in one trial. No significant  $\boldsymbol{\eta}_i$  terms were detected. The analyses revealed significant  $\hat{\sigma}_{g_i}^2$  for all trials. The  $\hat{r}_{gg_i}^2$  estimates ranged from 0.57 to 0.88 (mean = 0.77), with the lowest and highest values being obtained for trials 1 and 2, respectively.

An US form of  $\mathbf{G}_g$  did not provide a significantly better fit than the FA(1) model, suggesting that the latter was a satisfactory parsimonious model. In addition, as given in Table 5, the mean percentage of provenance variance accounted for by the regression behind the FA(1) model was 90%, with  $\hat{\psi}_i$  being equal to zero in two of the five trials. The fit of the FA(1) model was only marginally better (i.e.  $P = 0.05$ , 5df) than that of a FA(1)\_C structure, indicating that G x E interaction was not important for effects in  $\mathbf{u}_g$ .

On average, ST was best in trials 1, 2 and 5 (Table 5). A two-tailed LR test revealed a significant heterogeneity of  $\hat{\sigma}_{g_i}^2$ , with the smallest values being obtained for trials 1 and 5, where the reliability of effects in  $\mathbf{u}_g$  was also lower (i.e.  $\hat{r}_{gg_i}^2$  estimates of 0.57 and 0.73, respectively). In agreement with the minor G x E interaction suggested by statistically testing its significance, the  $\hat{\lambda}_i^c$  estimates were all high, indicating that the trials were well correlated. The average correlation between trials was 0.90.

Following the results mentioned above, the BLUPs of provenance effects obtained for ST at each trial were averaged, and the across-site means are presented in Table 9. In general, the straightest provenances were found amongst the sources from Vietnam

Madagascar and Zambia. The fact that the local source from Zambia was considerably better than the other seedlots may reflect the effect of earlier selection for ST. In this sense, the predicted superiority of 19% above the overall mean corresponded to an improvement of one class in the 1-9 classification system of ST, suggesting that this trait may have responded well to phenotypic selection. The two Burmese sources were poor performers for ST. The remaining sources did not show a clear pattern in terms of performance, but they tended to be either intermediate or inferior. In previous studies, *P. kesiya* provenances from Vietnam and/or Madagascar were also superior for ST, compared with sources from Philippines and Burma (Armitage and Burley, 1980, pages 47-54; Mullin *et al.*, 1984). The importance of improving ST in *P. kesiya* has been emphasized by Armitage and Burley (1980). In particular, for sawn timber production, these authors reported a 14% increase in economic value by improving one class in ST (for a 1-5 classification system). In addition, Hans and Williamson (1973) indicated that the percentage of compression wood decreased with the degree of stem sinuosity, and thus selection for ST may indirectly select against compression wood.

### *Branch diameter*

BD was measured in four trials (i.e. 1, and 3 to 5). Spatial analysis of BD revealed significant AR1 parameters across columns only for three trials, and included linear trends across rows and/or columns in  $\mathbf{b}$  for three trials, as well as column effects in  $\mathbf{u}_0$  for one trial. No significant  $\eta_i$  terms were detected. Significant  $\hat{\sigma}_{g_i}^2$  were found for all trials. The  $\hat{r}_{gg_i}^2$  estimates varied from 0.59 to 0.75 (mean = 0.65), with the lowest and highest values being obtained for trials 1 and 4, respectively.

The fit of the FA(1) model was not significantly poorer to that of the US form of  $\mathbf{G}_g$ , indicating that it was a suitable parsimonious model. As shown in Table 6, on average, the multiplicative part of the FA(1) model accounted for by 76% of the provenance variance, with  $\hat{\psi}_i$  being equal to zero in two trials. The G x E interaction

was statistically significant for effects in  $\mathbf{u}_g$ , as shown by comparing the fit of the FA(1) model with that of a FA(1)\_C structure.

Smaller BD is desirable for the production of high quality timber and, in this sense, trial 3 had the best average value (Table 6). A two-tailed LR test did not detect a significant heterogeneity for  $\hat{\sigma}_{g_i}^2$ , and the range of CV between trials was small. Following a tendency similar to VHA, the  $\hat{\lambda}_i^c$  estimates obtained for BD indicated that trial sites other than 1 had high pairwise provenance correlations. The mean across-site correlation between trial 1 and the others was 0.53, whereas the average correlation estimate for all trials except trial 1 was 0.90.

As shown for BD in Table 9, most of the provenances had only minor changes in rank between trial 1 and the group of trials 3 to 5. Nevertheless, relevant rank changes were apparent for sources 12, 22, 24 and, to a less extent, for seedlots 2, 9 and 14. The Philippines provenances and most of the Thai sources (i.e. 11, 13, 15 and 16) tended to have the smallest BD. Good performers for BD were also found amongst the Vietnamese provenances (i.e. 8 and 9). The sources from Madagascar and China tended to have the largest BD, whereas the Zambian seedlot and one of the Burmese provenances (i.e. 23) were intermediate. Previous studies in *P. kesiya* also reported that Philippines provenances were superior to Vietnamese and Burmese sources in their performance for BD (Armitage and Burley, 1980, pages 47-54). To conclude, the G x E interaction detected for BD was mainly caused by one site and, although the rankings changed to some extent, most of the provenances tended to have a consistent performance across trials. Therefore, it appears that, for the sites examined here, the practical importance of G x E interaction was not great for BD.

### *Forking*

FRK was measured in all trials. Spatial analysis of FRK found significant AR1 parameters across rows and/or columns for three trials (with a  $\eta_i$  term being included in one trial), and identified linear trends across rows and/or columns in  $\mathbf{b}$  for three trials, as well as column effects in  $\mathbf{u}_0$  for one trial. The  $\hat{\sigma}_{g_i}^2$  estimates were significant

for all trials except 1, 4 and 6. The mean incidence of FRK was also generally lower in trials 1, 4 and 6 than in the others (not shown). It was decided to discard these three trials from subsequent analysis, as they did not provide an adequate discrimination between provenances for FRK. For the remaining four trials, the  $\hat{r}_{gg_i}^2$  estimates ranged between 0.47 and 0.86 (mean = 0.66), with the lowest and highest values being obtained for trials 7 and 5, respectively.

Using an US form of  $\mathbf{G}_g$  did not lead to a significant improvement over the FA(1) model, suggesting that the latter would provide an adequate approximation to the full model. As supplied by Table 7, the mean percentage of provenance variance explained by the regression implied in the FA(1) model was about 70%, with  $\hat{\psi}_i$  being equal to zero in two trials. The comparison of the fit of the models FA(1) and FA(1)\_C indicated a statistically significant G x E interaction for effects in  $\mathbf{u}_g$ .

The trials tended to be similar in mean level of FRK, although the incidence of the trait was somewhat lower in trial 5 (Table 7). A two-tailed LR test did not detect a significant heterogeneity for  $\hat{\sigma}_{g_i}^2$ . The  $\hat{\lambda}_i^c$  estimates obtained for FRK pointed out that trial sites other than 5 tended to be well correlated. The average provenance correlation between trial 5 and the others was 0.42, whereas the mean estimate for all trials except trial 5 was 0.83.

The majority of the provenances had only minor alterations in ranking between trial 5 and the other trials (Table 9). The most marked ranking changes comprised provenances 5, 15, 17 and 21. The pattern of provenance performance in FRK tended to approach that described above for VHA and ST. In this sense, good performers in FRK included sources from Vietnam (i.e. 8, 9 and 10), Madagascar (i.e. 25 and 26) and Zambia. Seedlot 3 from the Philippines, which was intermediate for VHA and ST, performed also well for FRK. Conversely, the other Philippines sources tended to display a high incidence of FRK. The Burmese provenances were also poor performers for FRK. The Thai and Chinese sources did not demonstrate an apparent pattern in terms of performance but, in general, tended to be either intermediate or inferior. Concerning the practical importance of G x E interaction for the trials studied here, the conclusion made above for VHA and BD also applies for FRK.

## Foxtailing

Only trials 2, 3, 6 and 7 were analysed for FOX. Trial 1 was not measured for this trait, and the incidence levels of FOX were negligible in trials 4 and 5, precluding a meaningful assessment of provenance variance. Spatial analysis of FOX revealed significant AR1 parameters across columns only and for one trial (with a  $\eta_i$  term being retained), and identified linear trends across rows and/or columns in  $\mathbf{b}$  for two trials, as well as a spline term in  $\mathbf{u}_0$  for one trial. Significant  $\hat{\sigma}_{g_i}^2$  were detected for all trials. The  $\hat{r}_{gg_i}^2$  estimates ranged from 0.46 to 0.82 (mean = 0.62). The lowest  $\hat{r}_{gg_i}^2$  values were calculated for trials 3 and 7, whereas the highest estimates were obtained for trials 2 and 6.

There was a significant lack of fit in the FA(1) model compared with the US form of  $\mathbf{G}_g$ , and the average percentage of provenance variation explained by the regression implied in the FA(1) model was only 52%. This suggested that the addition of a second factor in the FA structure was required, as well as constraining the  $\hat{\psi}_i$  to be equal for preserving some benefit over the US form in terms of parsimony (i.e. 8 vs. 10 parameters). A two-tailed LR test did not detect significant heterogeneity for  $\hat{\psi}_i$  under the FA(1) model. Subsequently, the fit of the FA(2) model with the  $\hat{\psi}_i$  constrained to be equal was not significantly different from that of the US form. As provided by Table 8, the mean percentage of provenance variance accounted for by the multiplicative part of the FA(2) model was about 92%. Comparing the fit of this FA(2) model with that of a FA(1)\_C structure indicated that the G x E interaction was statistically significant for effects in  $\mathbf{u}_g$ .

As shown in Table 8, the mean incidence of FOX was high (i.e. 65%) in trial 7, moderate (i.e. 24%) in trial 6, and low (i.e. from 4% to 7%) in the other two trials. FOX arises from a pattern of continuous growth rather than the usual cyclical annual one; environmental conditions promoting FOX entail a year-round warm climate with an ample and well-distributed supply of rainfall (Armitage and Burley, 1980). As can be seen in Table 1, the mean level of FOX tended to be smaller for trial sites where the environmental features (i.e. lower values for PDM and for the minimum DR) suggest a



marked dry season. In particular, trial 7 seems to lack a distinct dry period (and thus the drought condition required for the apical meristem to produce lateral branch primordia), which may have allowed a continuous growth for a large percentage of the trees in the site. A two-tailed LR test did not detect a significant heterogeneity for  $\hat{\sigma}_{g_i}^2$ . Following an orthogonal rotation of the original factors, the magnitude of the  $\hat{\lambda}_i^c$  obtained for FOX indicated a contrast between two groups of sites - trials 2 and 6 (with greater emphasis on factor 1) versus trials 3 and 7 (with greater emphasis on factor 2) - in terms of the pattern of across-site correlations for effects in  $\mathbf{u}_g$  (Table 8). The mean correlation between the two trial groups was 0.34, whereas the estimates within groups were 0.86 (i.e. trials 2 and 6) and 0.76 (i.e. trials 3 and 7).

The BLUPs of provenance effects obtained for FOX at each trial were averaged for each of the two trial groups mentioned above, and the respective means are shown in Table 9. Pertinent ranking changes occurred for sources 13 and 15 from Thailand, 21 from China and 27 from Madagascar. Provenances 5, 8 and 9 from Vietnam also changed somewhat in rank, but these alterations may be unimportant as they occurred within the intermediate to poor range of the ranking performance. Explaining the changes in ranking on the basis of the available climatic information appears to be difficult, as the climatic conditions of the trial sites (Table 1) did not seem to be related with their grouping indicated by the pattern of across-site correlations. Information on additional environmental factors, such as photoperiod and radiation, could be helpful as they also have an influence on the physiological processes involved in growth rhythm. Nevertheless, there was a tendency for a lower level of FOX to be expressed in sources originating from localities with more severe drought conditions in the dry season (e.g. see PDM and minimum DR in Appendix 1). In this sense, the Vietnamese provenances were generally poor performers for FOX. This tendency also appeared in the Madagascar sources 25 and 26, which is not surprising given their Vietnamese origin. Conversely, the best performers for FOX were found amongst the sources from Burma, China and Thailand. Sources 3 and 4 from the Philippines were better performers than the other two provenances from the same country, and tended to be intermediate compared with the remaining sources. It is also interesting to note that the

Zambian seedlot performed reasonably well for FOX. To conclude, G x E interaction for FOX involved important changes in ranking for a few sources only, and patterns of provenance performance could be identified. Sites that lack a marked dry season (such as trial 7 and, to a less extent, trial 6) should be avoided for conducting experiments aiming at seed source selection, as they may not be suited for the establishment of *P. kesiya* plantations due to the propensity for the occurrence of FOX.

### *Analysis of pairs of traits*

As presented in Table 10, for a given trait pair, the common correlation between traits within trials was generally not significantly different from that across trials. The provenance correlations involving VHA, ST and FRK were significant, moderate to high, and their signs suggested that simultaneous improvement could be achieved in these traits following provenance selection (Table 10). Sources with favourable combinations of VHA, ST and FRK could be found amongst seedlots from Vietnam, Madagascar and Zambia (Table 9). However, the correlations between FOX and VHA, ST or FRK were adverse and significant (Table 10), indicating that provenance selection for improved growth rate and stem form could be accompanied by an increase of FOX in *P. kesiya* plantations. As indicated in Table 9, the Burmese, Chinese and Thai sources tended to display lower levels of FOX than seedlots from Vietnam. These results seemed to be related to the seasonal pattern of rainfall in the native seed collection sites, as the Vietnamese sources originated from localities where drought conditions (i.e. the amount and distribution of rainfall) in the dry season were milder than the other native stand localities. Thus, site choice may be of crucial importance for deploying provenance material selected for improved growth rate and timber quality. In this sense, plantation sites with a distinct seasonal pattern of rainfall may be more appropriate for minimizing the incidence of stem defects such as FOX.

PIL was generally poorly and not significantly correlated with the other traits (Table 10). Despite the substantial G x E interaction found for PIL, there was only one case (i.e. for the pair PIL/FRK) where the common between-trait correlation within trials was significantly different from the corresponding estimate across trials. Yet,

low and non-significant estimates were also obtained for pooled correlations between traits using only the information from trials 3 to 5, where the across-site correlations were high for PIL (Table 4). In this context, between-trait correlations of PIL with VHA, ST and BD were 0.17 ( $\pm$  0.22), -0.01 ( $\pm$  0.24) and -0.18 ( $\pm$  0.25), respectively (not shown). These results indicate that wood density in the juvenile core of *P. kesiya* may be improved by provenance selection without important indirect reductions in gain for other wood quality traits and growth rate. In a study involving *P. kesiya* provenances, Mullin *et al.* (1984) also reported that there were no significant correlations between basic density at 6½ years and growth traits or stem straightness. Following a tendency similar to PIL, the correlations between BD and the other traits were low and not significantly different from zero (Table 10).

The patterns of provenance performance illustrated in Table 9 for individual traits were reflected reasonably well in the estimated provenance correlations between traits. Concerning the economic effect of improving diameter growth, stem form and branch characteristics for sawn timber production, results reported by Armitage and Burley (1980) in *P. kesiya* indicated that the greatest economic gains were achieved by increasing stem straightness and growth rate; the economic gain obtained by reducing branch diameter was small compared with the other two traits. In this sense, the results obtained in the present study suggested that the Zambian CSO source could supply seed of superior quality for a range of conditions, as it had favourable combinations of traits (such as good VHA, ST, FRK and FOX, as well as an intermediate performance for BD) and was fairly stable across several environments. The Vietnamese sources 8 and 9 also performed simultaneously well for VHA, ST, BD and FRK. In addition, *P. kesiya* has a large juvenile core with undesirable wood properties (Armitage and Burley, 1980) and, in this context, wood density may be an important trait to consider in breeding programmes that aim at improving the production of structural timber. The sources 7 and 8 from Vietnam, as well as the seedlot 25 from Madagascar, tended to have an intermediate performance for PIL, while having desired trait combinations for VHA, ST and FRK.

## Conclusion

Analysis of early data from the *P. kesiya* provenance trials in this study demonstrated high survival rates and vigorous growth as an exotic species under a range of tropical and subtropical conditions in several countries. There was significant provenance variance for growth rate, as well as for an array of wood quality traits such as Pilodyn penetration, stem straightness, branch diameter, forking and foxtailing. A strong G x E interaction was detected for Pilodyn penetration, but it is likely to be confounded by the presence of a provenance by time interaction in wood density due to possible differences between provenances in the radial pattern of age variation for this wood property within the juvenile core. Further Pilodyn assessments at a later age will be needed for more effective seed source selection for wood density. Patterns of provenance performance could be identified for the other traits, and the practical importance of G x E interaction seemed to be small, usually not involving relevant ranking changes for the majority of the tested sources.

The results indicated that the native *P. kesiya* sources from Vietnam could have an important value for provenance research and breeding, as they provided favourable combinations of growth and wood quality traits. Local seedlots from Madagascar and Zambia also displayed desirable trait combinations, and thus could be considered as valuable sources for seed supply and breeding. However, as total volume per hectare and stem straightness appeared to be significantly negatively correlated with foxtailing, site choice may be of crucial importance for minimizing the occurrence of these stem defects while deploying provenance material selected for improved growth rate and timber quality. Finally, the populations tested in this study may represent restricted fractions of the natural distribution of *P. kesiya*, and thus further research with a better coverage of the species range may be required for an efficient exploitation of the available provenance variation.

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**TABLE 1** - Location, climate and data information for each *Pinus kesiya* trial site.

Trial	Latitude	Longitude	Altitude (m)	Precipitation (mm)			Temperature (°C)			RH (%)	MAI	DR (days/month)	Establ.-Meas. Years	Mean Survival (%)
				AP	PDM	PWM	AMT	MTWM	MTCM					
Ba Vi, Vietnam (1)	21°06'N	105°26'E	520	1693.8	7.8	427.0	24.7	30.0	17.7	82.9 (80 - 85)	0.71 (0.015 - 1.72)	12.6 (5.1 - 18.1)	1993 -1998 (5 years)	75.0
Cashel, Zimbabwe (2)	19°33'S	32°47'E	1450	941.6	1.3	324.1	18.3	21.3	14.1	73.8 (63 - 83)	0.37 (0.018 - 0.99)	9.1 (4.1 - 15.5)	1992 - 1998 (6 years)	99.1
Grootgeluk, South Africa (3)	25°34'S	30°38'E	1200	969.2	2.4	268.0	17.0	20.9	11.5	63.4 (54 - 71)	0.35 (0.002 - 0.76)	7.3 (1.5 - 13.4)	1991 - 1998 (7 years)	98.6
R136_G, Swaziland (4)	26°32'S	31°02'E	800	851.0	3.2	197.6	18.8	22.4	14.4	66.5 (55 - 74)	0.34 (0.003 - 0.73)	7.7 (1.8 - 13.8)	1990 - 1998 (8 years)	85.1
R136_J, Swaziland (5)	26°37'S	31°02'E	1100	851.0	3.2	197.6	18.8	22.4	14.4	66.5 (55 - 74)	0.34 (0.003 - 0.73)	7.7 (1.8 - 13.8)	1990 - 1998 (8 years)	97.6
Granada, Colombia (6)	02°35'N	76°53'W	2100	1850.9	27.0	327.4	18.6	19.4	17.8	84.4 (79 - 88)	1.94 (0.38 - 4.33)	17.4 (8.6 - 23.2)	1990 - 1998 (8 years)	90.3
Romerito, Colombia (7)	03°43'N	76°32'W	1400	1756.6	50.9	269.0	22.7	23.3	21.9	81.1 (79 - 83)	0.64 (0.30 - 1.24)	17.0 (12.5 - 21.9)	1990 - 1998 (8 years)	96.5

*Note:* Each trial has a number in parenthesis, for purposes of its identification in this study. The years of establishment and measurement are presented for each trial, and the measurement age given in parenthesis applies to all traits evaluated in the trial. Using latitude and longitude coordinate values as input data, climatic records were obtained from the integrated database information system of the International Water Management Institute (<http://dw.iwmi.org/dataplatform/ClickandPlot.aspx>). For the precipitation and temperature variables, the values listed pertain to averages taken over the years of the period from the trial establishment to its measurement. For RH, MAI and DR, the data available in the database consisted of monthly averages corresponding only to the period from 1961 to 1990, and the overall means (with the minimum and maximum monthly averages in parentheses) are presented. AP - Annual precipitation; PDM - Precipitation of the driest month; PWM - Precipitation of the wettest month; AMT - Annual mean temperature; MTWM - Mean temperature of the warmest month; MTCM - Mean temperature of the coldest month; RH - Relative humidity; MAI - Hargreaves Moisture Availability Index (i.e. an indicator of the water availability in the soil - Hargreaves 1975); DR - Days with rainfall.



**TABLE 2** - Number of provenances of *Pinus kesiya* tested in each trial (diagonal) and number of provenances in common amongst trials (off-diagonal).

	Trial 1	Trial 2	Trial 3	Trial 4	Trial 5	Trial 6	Trial 7
Trial 1	16						
Trial 2	8	17					
Trial 3	12	12	22				
Trial 4	8	12	12	16			
Trial 5	8	12	12	16	16		
Trial 6	8	14	15	14	14	19	
Trial 7	11	14	18	15	15	19	22

**TABLE 3** - Parameter estimates from a FA(1) model applied to the across-site analysis of total volume per hectare measured in seven *Pinus kesiya* trials. Approximated standard errors are given in parenthesis for the absolute  $\hat{\sigma}_{g_i}^2$ .

Trial	Mean (m <sup>3</sup> /ha)	$\hat{\sigma}_{g_i}^2$		$\hat{\lambda}_i$	$\hat{\lambda}_i^c$	$\hat{\psi}_i$	VE (%)
		Abs.	CV (%)				
1	30.3	20.3 (11.0)	14.9	2.09	0.464	15.9	21.5
2	80.8	133.2 (43.4)	14.3	11.54	1.0	0.0	100.0
3	108.7	427.1 (147.3)	19.0	17.32	0.838	127.1	70.2
4	133.9	339.0 (143.1)	13.7	15.62	0.848	95.0	71.9
5	127.3	117.4 (68.7)	8.5	10.70	0.987	2.9	97.4
6	221.4	1214.9 (474.7)	15.7	30.42	0.873	289.5	76.2
7	132.7	281.3 (130.9)	12.6	14.10	0.841	82.5	70.7

**TABLE 4** - Parameter estimates from a FA(1) model applied to the across-site analysis of Pilodyn penetration measured in five *Pinus kesiya* trials. Approximated standard errors are given in parenthesis for the absolute  $\hat{\sigma}_{g_i}^2$ .

Trial	Mean (mm)	$\hat{\sigma}_{g_i}^2$		$\hat{\lambda}_i$	$\hat{\lambda}_i^c$	$\hat{\psi}_i$	VE (%)
		Abs.	CV (%)				
1	29.6	0.65 (0.46)	2.7	-0.277	-0.344	0.574	11.8
2	22.4	0.84 (0.30)	4.1	-0.886	-0.967	0.053	93.5
3	18.5	0.42 (0.20)	3.5	0.643	0.992	0.006	98.4
4	21.2	0.47 (0.22)	3.2	0.687	1.0	0.0	100
5	17.0	0.57 (0.24)	4.4	0.755	1.0	0.0	100

**TABLE 5** - Parameter estimates from a FA(1) model applied to the across-site analysis of stem straightness measured in five *Pinus kesiya* trials. Approximated standard errors are given in parenthesis for  $\hat{\sigma}_{g_i}^2$ .

Trial	Mean (score)	$\hat{\sigma}_{g_i}^2$	$\hat{\lambda}_i$	$\hat{\lambda}_i^c$	$\hat{\psi}_i$	VE (%)
1	6.6	0.13 (0.06)	0.364	1.0	0.0	100
2	6.5	0.22 (0.07)	0.424	0.904	0.043	81.7
3	5.7	0.17 (0.06)	0.403	0.977	0.007	95.5
4	5.9	0.27 (0.10)	0.450	0.866	0.065	75.0
5	6.4	0.08 (0.04)	0.284	1.0	0.0	100

**TABLE 6** - Parameter estimates from a FA(1) model applied to the across-site analysis of branch diameter measured in four *Pinus kesiya* trials.

Approximated standard errors are given in parenthesis for the absolute  $\hat{\sigma}_{g_i}^2$ .

Trial	Mean (cm)	$\hat{\sigma}_{g_i}^2$		$\hat{\lambda}_i$	$\hat{\lambda}_i^c$	$\hat{\psi}_i$	VE (%)
		Abs.	CV (%)				
1	2.8	0.042 (0.024)	7.3	0.116	0.566	0.029	32.0
3	2.3	0.051 (0.022)	9.8	0.191	0.846	0.014	71.6
4	2.7	0.057 (0.025)	8.8	0.239	1.0	0.0	100
5	3.4	0.068 (0.032)	7.7	0.260	1.0	0.0	100

**TABLE 7** - Parameter estimates from a FA(1) model applied to the across-site analysis of forking measured in four *Pinus kesiya* trials.

Approximated standard errors are given in parenthesis for  $\hat{\sigma}_{g_i}^2$ .

Trial	Mean (%)	$\hat{\sigma}_{g_i}^2$	$\hat{\lambda}_i$	$\hat{\lambda}_i^c$	$\hat{\psi}_i$	VE (%)
2	35.5	66.8 (31.2)	6.14	0.751	29.1	56.4
3	34.1	149.6 (70.2)	12.23	1.0	0.0	100
5	23.9	156.7 (65.6)	5.77	0.461	123.4	21.2
7	34.9	113.2 (62.8)	10.64	1.0	0.0	100

**TABLE 8** - Parameter estimates from a FA(2) model applied to the across-site analysis of foxtailing measured in four *Pinus kesiya* trials. Except for the trial means, which were transformed back to the original scale, the parameter estimates presented are based on transformed data.  $\hat{\lambda}_i$  and  $\hat{\lambda}_i^c$  for factors 1 and 2 correspond to loadings obtained after an orthogonal rotation of the original factors. Approximated standard errors are given in parenthesis for  $\hat{\sigma}_{g_i}^2$ .

Trial	Mean (%)	$\hat{\sigma}_{g_i}^2$ (0.010)	$\hat{\lambda}_{i_1}$	$\hat{\lambda}_{i_2}$	$\hat{\lambda}_{i_1}^c$	$\hat{\lambda}_{i_2}^c$	$\hat{\psi}_i$	VE (%)
2	6.7	0.024 (0.010)	0.139	0.061	0.897	0.394	0.001	96.0
3	4.2	0.008 (0.004)	-0.002	0.081	-0.022	0.906	0.001	82.1
6	23.9	0.028 (0.015)	0.165	-0.004	0.986	-0.024	0.001	97.3
7	65.0	0.013 (0.009)	0.048	0.100	0.421	0.877	0.001	94.6

**TABLE 9** - Best linear unbiased predictors of provenance effects (PV) and provenance ranks (R) for several traits measured in *Pinus kesiya* trials.

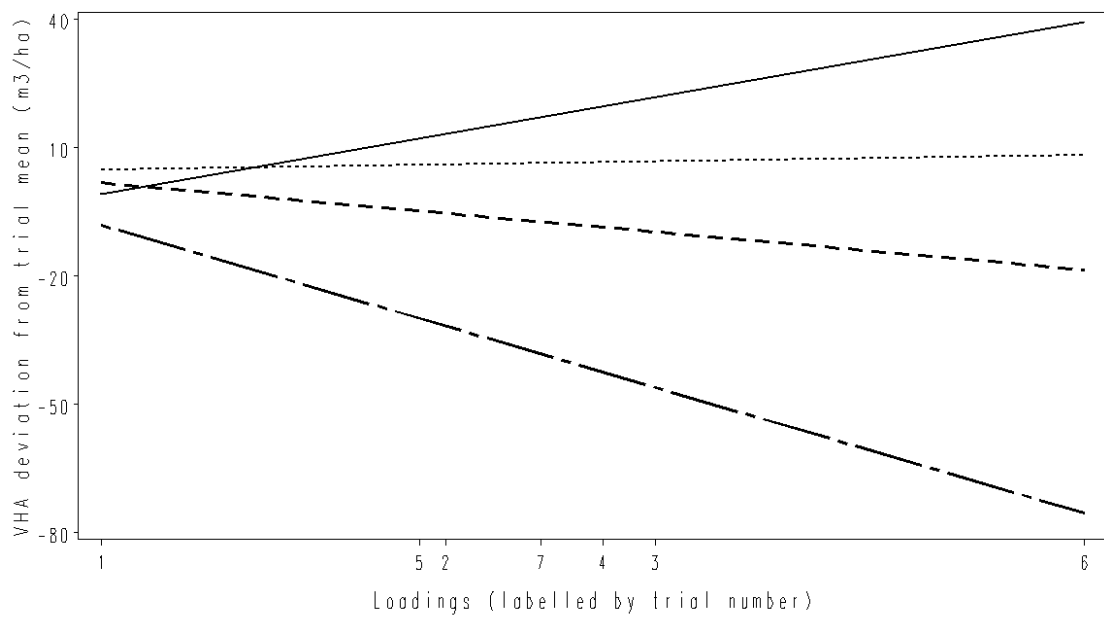
Prov. code	SUR		VHA				PIL						ST		BD				FRK				FOX			
	1 to 7		1		2 to 7		1		2		3 to 5		1 to 5		1		3 to 5		5		2, 3 and 7		2 and 6		3 and 7	
	PV	R	PV	R	PV	R	PV	R	PV	R	PV	R	PV	R	PV	R	PV	R	PV	R	PV	R	PV	R	PV	R
1	2.29	1	-0.19	18	0.81	18	-1.16	5	-4.80	5	4.56	25	-3.15	20	-7.89	3	-15.86	1	6.47	19	16.47	19	14.27	21	8.49	20
2	0.19	14	-1.60	21	6.09	10	-2.82	3	-5.29	3	4.60	26	-2.83	19	-0.83	11	-8.61	3	-5.64	14	17.58	21	35.27	23	8.80	21
3	-0.02	15	3.07	13	3.49	13	-4.21	1	-8.41	1	7.85	28	-0.31	13	-7.53	4	-10.44	2	-34.81	5	-40.03	1	4.64	19	1.38	15
4	-1.75	25	-22.19	26	5.19	11	0.12	12	-7.96	2	6.87	27	4.14	7	-2.52	8	-1.58	11	34.80	27	46.58	28	3.18	17	0.79	14
5	-0.24	20	8.42	4	11.38	5	0.60	19	2.34	20	-2.35	8	5.67	4	1.15	16	1.61	16	17.47	22	-23.66	5	64.36	28	8.22	19
6	-0.23	19	13.38	2	9.15	7	0.79	21	-1.48	9	1.38	20	5.66	5	2.66	18	0.57	15	0.36	17	0.41	17	0.77	15	2.09	16
7	1.08	6	5.99	7	12.84	4	0.13	13	0.63	14	-0.52	15	1.63	9	1.09	15	2.39	18	-9.07	11	-12.09	12	49.59	27	23.32	28
8	0.98	7	-0.25	19	18.39	1	-1.00	6	1.47	16	-1.35	11	4.04	8	-2.21	9	-5.67	8	-14.50	8	-16.58	9	3.96	18	14.89	25
9	0.60	13	5.75	8	7.29	9	2.15	27	0.11	12	-0.40	16	7.17	3	-8.30	1	-6.37	7	-29.61	6	-15.38	11	-1.68	13	12.23	23
10	0.70	10	7.76	5	14.63	2	0.33	16	1.17	15	-1.32	12	-1.36	15	3.32	19	7.31	22	-26.27	7	-28.18	4	42.89	26	19.07	26
11	1.45	4	0.35	16	-8.55	23	1.51	24	2.65	21	-1.81	9	-3.17	21	-7.95	2	-7.11	6	-6.21	12	-16.61	8	-38.95	4	-15.82	3
12	-0.18	17	-2.37	22	2.79	14	1.28	22	1.87	19	-1.75	10	-1.44	16	5.77	24	-1.87	10	-5.77	13	-6.63	14	-14.88	8	-9.65	7
13	0.68	12	14.69	1	2.45	15	2.60	28	3.47	25	-4.36	3	-4.96	23	-4.98	7	-7.82	4	10.89	20	-5.57	15	-29.20	5	2.64	17
14	1.38	5	-0.66	20	-2.01	19	0.44	17	3.98	26	-3.72	4	-3.42	22	8.10	27	3.05	19	-14.34	9	-16.50	10	10.58	20	13.83	24
15	2.13	2	4.22	11	-8.37	22	1.78	26	1.72	18	-1.08	13	0.14	12	-6.70	6	-7.49	5	26.26	25	-28.32	3	-61.20	2	20.36	27
16	0.82	8	5.03	10	-4.37	21	0.22	14	5.16	27	-4.82	2	-2.37	18	-7.46	5	-4.87	9	22.49	24	25.87	23	-2.15	12	-5.84	11
17	-0.21	18	-10.02	25	-20.88	26	-0.77	7	-3.27	6	3.00	23	-6.42	26	5.44	23	11.67	26	-48.79	3	30.85	25	-27.58	6	-23.12	2
18	-0.15	16	-8.62	24	-17.49	25	1.52	25	6.86	28	-5.97	1	-6.92	27	NA	NA	NA	NA	14.33	21	16.95	20	-18.83	7	-7.56	10
19	0.72	9	-2.85	23	-12.85	24	-0.43	10	0.16	13	-0.15	17	-5.08	24	7.55	26	5.93	20	4.41	18	5.07	18	-1.01	14	-4.96	12
20	-1.66	24	1.23	15	0.92	17	0.61	20	2.92	23	-2.37	7	-0.78	14	2.46	17	6.41	21	-3.98	16	-11.20	13	-12.81	10	-3.84	13
21	1.65	3	2.41	14	1.84	16	0.59	18	2.96	24	-2.38	6	-2.31	17	3.72	20	7.93	24	-11.68	10	27.09	24	2.54	16	-12.78	4
22	0.69	11	12.58	3	-3.58	20	-3.44	2	2.66	22	-2.49	5	0.50	11	6.50	25	0.13	14	34.62	26	39.83	26	-3.29	11	-8.95	9
23	-0.89	23	-24.75	27	-27.17	28	-1.52	4	-4.86	4	4.16	24	-5.29	25	-1.66	10	-1.32	12	159.83	28	44.42	27	-55.57	3	-28.27	1
24	-4.19	28	-26.57	28	-26.47	27	1.48	23	-1.03	10	1.10	19	-12.18	28	-0.35	12	12.64	27	22.43	23	22.31	22	-62.49	1	-11.95	6
25	-0.84	22	5.05	9	9.39	6	-0.05	11	-0.22	11	0.22	18	4.91	6	4.28	21	7.78	23	-35.87	4	-22.92	6	40.30	25	9.96	22
26	-2.11	26	3.78	12	7.99	8	-0.58	8	-2.48	7	2.30	22	1.38	10	4.77	22	9.46	25	-50.88	2	-18.19	7	33.29	22	8.21	18
27	-0.71	21	0.01	17	3.63	12	0.24	15	1.60	17	-0.91	14	7.78	2	1.04	14	2.29	17	-5.43	15	-2.75	16	37.59	24	-9.20	8
28	-2.19	27	6.34	6	13.48	3	-0.44	9	-1.93	8	1.72	21	19.01	1	0.54	13	-0.16	13	-51.55	1	-28.80	2	-13.59	9	-12.33	5

*Note:* For each trait, the PV values are presented as single-trial estimates or as averages for groups of trials, with the trial partition being based on the patterns of provenance by environment interaction indicated by the across-site analyses. The PV values are expressed in percentage of the mean of the single trials or groups of trials. For PIL, BD, FRK and FOX, the provenance ranking is in ascending order (i.e. the higher ranking is given for lower PV values), as provenance selection aims at reducing the levels of these traits. For SUR and FOX, the PV values were calculated on a transformed scale, and then expressed in percentage of the means of the transformed data. SUR - Survival; VHA - Total volume per hectare; PIL - Pilodyn penetration; ST - Stem straightness; BD - Branch diameter; FRK - Forking; FOX - Foxtailing. NA - Provenance not tested in trials 1 and 3 to 5, where BD was measured.

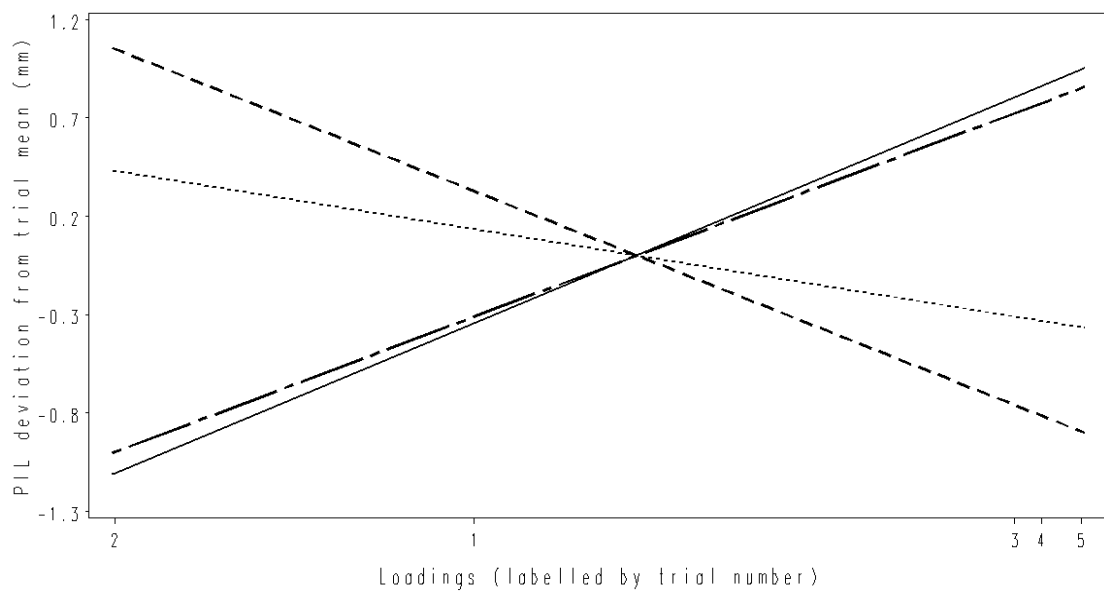
**TABLE 10** - Provenance correlations estimated between traits, based on bivariate analyses of *Pinus kesiya* trials.

	VHA	PIL	ST	BD	FRK
PIL	-0.08 <sup>a)</sup> (0.05) $P>0.05$				
ST	0.62 <sup>a)</sup> (0.09) $P\leq 0.001$	0.01 <sup>a)</sup> (0.06) $P>0.05$			
BD	-0.19 <sup>b)</sup> (0.18) $P>0.05$	-0.21 <sup>b)</sup> (0.18) $P>0.05$	-0.02 <sup>b)</sup> (0.20) $P>0.05$		
FRK	-0.60 <sup>b)</sup> (0.09) $P\leq 0.001$	-0.23 <sup>c)</sup> (0.09) $P\leq 0.05$	0.15 <sup>c)</sup> (0.08) $P>0.05$	-0.35 <sup>c)</sup> (0.17) $P\leq 0.05$	-0.17 <sup>d)</sup> (0.23) $P>0.05$
FOX	0.64 <sup>b)</sup> (0.07) $P\leq 0.001$	0.01 <sup>d)</sup> (0.11) $P>0.05$	0.38 <sup>d)</sup> (0.17) $P\leq 0.05$	0.19 <sup>e)</sup> (0.42) $P>0.05$	-0.50 <sup>c)</sup> (0.17) $P\leq 0.05$

*Note:* For the trait pair PIL/FRK, the common correlation within trials (left side) was significantly different ( $P\leq 0.05$ ) from the estimate across trials (right side). For the other trait pairs, and excepting the pair BD/FOX (where only one trial was used for estimation), the common correlations between traits within trials did not differ significantly from those across trials and, therefore, an estimated pooled value is presented. For each correlation estimate, an approximated standard error is given in parenthesis, and the significance probability pertain to a two-tailed likelihood ratio test applied to assess whether or not it deviates significantly from zero. VHA - Total volume per hectare; PIL - Pilodyn penetration; ST - Stem straightness; BD - Branch diameter; FRK - Forking; FOX - Foxtailing. <sup>a)</sup>, <sup>b)</sup>, <sup>c)</sup>, <sup>d)</sup> and <sup>e)</sup> - estimates based on data from five, four, three, two and one trial, respectively.



**FIGURE 1** - FA(1) model for provenances effects in each trial: total volume per hectare. Fitted regression lines are depicted against the trial loadings for four provenances. Provenances: 8 (——); 13 (·····); 15 (---); 23 (-·-·-).



**FIGURE 2** - FA(1) model for provenances effects in each trial: Pilodyn penetration. Fitted regression lines are depicted against the trial loadings for four provenances. Provenances: 2 (——); 11 (·····); 13 (---); 23 (-·-·-).

**APPENDIX 1 - *Pinus kesiya* provenances represented in the field trials, and description of the location and climate of their seed collection site.**

Provenance	Code	Country	Latitude	Longitude	Altitude (m)	Precipitation (mm)			Temperature (°C)			RH (%)	MAI	DR (days/month)	Representation in field trials
						AP	PDM	PWM	AMT	MTWM	MTCM				
Mt. Province	1	Philippines	17°15'N	120°55'E	2300	2601.9	4.3	763.3	22.4	29.2	15.0	83.5 (79-90)	1.36 (0.024-3.98)	14.2 (4.6-25.5)	2, 3, 4, 5, 6, 7
Benguet	2	Philippines	16°35'N	120°30'E	1600	2877.4	14.4	688.8	25.7	32.3	18.7	79.2 (74-87)	0.82 (0.0003-2.98)	10.4 (1.1-23.4)	1, 2, 4, 5
Tarlac	3	Philippines	15°23'N	120°08'E	1120	2438.2	<0.1	699.2	24.3	31.2	17.5	79.3 (72-88)	1.29 (0.0007-5.33)	11.7 (0.7-26.5)	1, 3, 6, 7
Coto Mines	4	Philippines	15°32'N	120°05'E	800	2392.3	<0.1	713.2	25.3	32.5	17.9	79.2 (72-88)	1.26 (0.0005-5.21)	11.5 (0.6-26.3)	1, 2
Dathien	5	Vietnam	11°58'N	108°27'E	1550	1868.9	16.6	356.5	21.7	28.3	12.8	74.9 (69-81)	0.85 (0.023-1.83)	14.9 (5.8-23.7)	2, 3, 4, 5, 6, 7
Xuan Tho	6	Vietnam	11°55'N	108°32'E	1400	1850.9	20.0	367.7	23.2	30.3	13.8	75.0 (69-81)	0.79 (0.024-1.77)	15.0 (5.9-23.7)	1, 3
Ho Tien	7	Vietnam	11°51'N	108°32'E	1500	1850.9	20.0	367.7	23.2	30.3	13.8	75.0 (69-81)	0.79 (0.024-1.77)	15.0 (5.9-23.7)	2, 3, 6, 7
Thac Prenn	8	Vietnam	11°52'N	108°27'E	1250	1868.9	16.6	356.5	21.7	28.3	12.8	74.9 (69-81)	0.85 (0.023-1.83)	14.9 (5.8-23.7)	1, 3, 4, 5, 7
Lang Hanh	9	Vietnam	11°37'N	108°16'E	950	1868.9	16.6	356.5	21.7	28.3	12.8	74.6 (68-81)	0.79 (0.014-1.72)	14.3 (5.3-22.3)	1, 2, 4, 5, 6, 7
Dakha	10	Vietnam	14°48'N	107°56'E	1200	2044.7	21.8	436.7	21.4	27.8	10.7	75.7 (71-81)	0.84 (0.050-2.55)	13.5 (4.7-25.6)	2, 3
Nong Krating	11	Thailand	18°05'N	98°35'E	1080	1101.1	0.5	260.8	25.5	36.6	12.8	72.4 (54-82)	0.53 (0.0001-1.47)	10.8 (0.8-22.6)	1, 2, 2, 3, 4, 5, 6, 7
Doi Suthep	12	Thailand	18°46'N	98°53'E	1300	1143.9	0.7	266.0	23.9	34.7	11.1	71.9 (53-82)	0.53 (0.0002-1.49)	10.2 (1.0-21.4)	1, 3, 6, 7
Doi Inthanon	13	Thailand	18°32'N	98°35'E	1000	1143.9	0.7	266.0	23.9	34.7	11.1	70.7 (52-81)	0.61 (0.0002-1.67)	11.8 (1.5-24.7)	1, 2, 4, 5, 6, 7
Phu Kradung	14	Thailand	16°51'N	101°47'E	1250	1103.0	0.1	257.9	25.2	34.9	12.9	71.7 (60-82)	0.53 (<0.0001-1.51)	10.8 (1.5-20.5)	1, 3, 7
Nam Now	15	Thailand	16°40'N	101°33'E	800	1103.0	0.1	257.9	25.2	34.9	12.9	71.1 (59-82)	0.53 (<0.0001-1.58)	10.8 (1.6-20.6)	1, 2, 3, 4, 5, 6, 7
Wat Chan	16	Thailand	19°04'N	98°19'E	940	1256.4	0.6	295.5	22.5	33.6	9.6	69.5 (50-81)	0.70 (0.0001-1.98)	12.1 (1.5-25.8)	1, 3
Jingdung (1)	17	China	24°26'N	100°51'E	1300	1124.8	4.2	275.7	16.9	26.8	2.6	71.0 (55-82)	0.53 (0.028-1.47)	13.3 (4.0-24.7)	3, 4, 5, 6, 7
Jingdung (2)	18	China	24°28'N	100°51'E	1350	1124.8	4.2	275.7	16.9	26.8	2.6	71.0 (55-82)	0.53 (0.028-1.47)	13.3 (4.0-24.7)	2, 6, 7
Jingdung Arb	19	China	24°28'N	101°05'E	1200	1112.7	3.4	281.2	16.1	26.4	1.8	69.4 (53-81)	0.59 (0.032-1.65)	13.8 (4.6-25.3)	1, 3, 7
Jinghong	20	China	22°25'N	101°10'E	1250	1365.4	4.8	329.8	20.2	29.9	7.5	75.0 (60-80)	0.87 (0.051-2.57)	13.0 (3.8-24.9)	2, 3, 4, 5, 6, 7
Lancang	21	China	22°40'N	100°03'E	1620	1349.0	3.5	328.2	18.6	28.8	4.7	71.7 (53-83)	0.89 (0.032-2.67)	13.3 (3.3-25.7)	2, 3, 4, 5, 6, 7
Simao	22	China	22°50'N	101°00'E	1370	1416.2	5.1	346.6	19.6	29.7	6.0	73.8 (58-83)	0.88 (0.047-2.60)	13.4 (3.9-25.3)	1, 3
Zokhua	23	Burma	22°25'N	93°40'E	1600	2576.5	1.7	637.5	19.8	27.9	8.2	71.9 (57-85)	1.59 (0.001-4.70)	9.6 (1.1-20.6)	1, 2, 3, 4, 5, 6, 7
Aungban	24	Burma	20°41'N	96°37'E	1350	1554.7	0.7	360.2	20.2	30.5	8.1	59.6 (38-75)	0.71 (0.0002-1.84)	10.4 (1.2-22.2)	1, 2, 3, 4, 5, 6, 7
Bodana A8	25	Madagascar	20°35'S	47°30'E	1500	1362.3	10.8	351.6	17.1	24.3	9.2	81.1 (76-84)	0.55 (0.074-1.43)	13.5 (6.3-20.5)	3, 4, 5, 6, 7
Bodana A9	26	Madagascar	20°35'S	47°30'E	1500	1362.3	10.8	351.6	17.1	24.3	9.2	81.1 (76-84)	0.55 (0.074-1.43)	13.5 (6.3-20.5)	4, 5, 6, 7
Morarano	27	Madagascar	18°40'S	47°02'E	900	1362.6	2.1	379.0	18.2	25.5	9.6	77.5 (72-82)	0.53 (0.004-1.59)	10.3 (2.5-19.7)	2, 3, 6, 7
CSO	28	Zambia	13°00'S	28°00'E	1300	1302.1	<0.1	354.4	19.7	31.4	4.6	64.7 (42-81)	0.21 (<0.0001-0.99)	8.7 (0.0-22.5)	2, 3, 4, 5, 6, 7

Note: Using latitude and longitude coordinates as input data, climatic values were obtained from the integrated database information system of the International Water Management Institute (<http://dw.iwmi.org/dataplatform/ClickandPlot.aspx>), and pertain to averages taken over the years of the period from 1961 to 1990 (for RH, MAI and DR, the minimum and the maximum monthly averages are given in parenthesis). AP - Annual precipitation; PDM - Precipitation of the driest month; PWM - Precipitation of the wettest month; AMT - Annual mean temperature; MTWM - Mean temperature of the warmest month; MTCM - Mean temperature of the coldest month; RH - Relative humidity; MAI - Hargreaves Moisture Availability Index (i.e. an indicator of the water availability in the soil - Hargreaves 1975); DR - Days with rainfall. See Table 1 for the identification (with codes from 1 to 7) of the field trials where provenances were tested.





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