# EFFECTS OF PROVENANCE AND GENETIC VARIATION ON THE GROWTH AND STEM FORMATION OF *EUCALYPTUS PELLITA* IN COLOMBIA

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**NIETO V, GIRALDO-CHARRIA D, SARMIENTO M & BORRALHO N. 2016. Effects of provenance and genetic variation on the growth and stem formation of *Eucalyptus pellita* in Colombia.** The study reports a genetic analysis of growth and stem formation of *Eucalyptus pellita* in Orinoquia, eastern Colombia. Families from two restricted locations in New Guinea, collected ex-situ in a local arboretum, significantly outperformed four Queensland, Australia provenances for growth and stem formation. Heritability estimates were low for both traits, 0.05–0.10. Correlation between stem straightness and diameter was positive and strong, but null with height despite height and diameter being strongly related. The mixed model used fitted a spatial component, allowing the estimate of autocorrelations of residuals between neighbouring trees. Autocorrelations changed from slight positive at 1 year old, an indication that the microsite conditions were homogeneous, to moderately negative at age two years onwards, especially for diameter, suggesting competition was starting to impact the performance of neighbouring trees at as early as 2 years old. Despite the reduced size of collection and the possible biases caused by prior ex-situ selection of New Guinea, compared with the native Queensland seed lots, the marked differences found suggested New Guinea sources to be better adapted to local wet and hot conditions.

Keywords: Heritability, provenance/progeny trial, REML variance components, spatial analysis

## INTRODUCTION

The eastern plains of Colombia, known as Orinoquia, have the greatest forestry potential in the country. With its 5–6 million ha suitable for afforestation, it is likely to become a future eucalypt plantation hotspot (Anonymous 1998). The Orinoquia extends from the lower slopes of eastern Cordillera to the Orinoco River, some 800 km eastwards, at the border of Venezuela. It is a strip of land known locally as Piedemonte, at altitude between 500 and 700 m above sea level. One of the earliest plantation forestry species to be tested in Orinoquia was *Eucalyptus pellita* by Reforestadora de la Costa (Refocosta), an integrated forest and wood products company operating in Colombia since 1980. The company's forest estate is located in east Orinoquia, near Villanueva town, in the Colombian district of Casanare (Figure 1).

In recent years there has been increasing interest in establishing eucalypt plantations in the region. By 2012, the area of *E. pellita* in Orinoquia was estimated to have reached 20,000 ha (Corporación Nacional de Investigación y Fomento Forestal, personal communication). These eucalypt plantations were established with a broad spectrum of possible end uses, including export of logs for pulp, charcoal or energy. Locally, it has been mainly used as utility poles for telephone links or electrical power lines and other agricultural structures such as fence posts.

The climate in Orinoquia changes from very humid conditions near the foothills of cordillera, with 3000 mm annual precipitation, to a drier and more seasonal climate in the flat lands to the east, with mean rainfalls between 1800 to 2000 mm and a more pronounced dry period extending up to 2–3 months. Across the region, mean daily temperatures range between 23 and 30 °C. Therefore, Orinoquia

 


**Figure 1** The Orinoquia region in Colombia and the experimental site near Villanueva

is classified as tropical wet and dry or savanna (Aw type) and foothill of cordillera is classified as tropical monsoon (Am type) according to Köppen classification system (Kottek et al. 2006).

Although *E. pellita* proved to be well adapted to tropical wet conditions, little is known about provenances that are suitable. This is important for the species since its native range includes three main genetic groups i.e. New Guinea, Cape York and Queensland and several studies worldwide have reported significant genetic differentiation between them (Harwood 1998, Brawner et al. 2013). In a recent taxonomic study of the species, Hill and Johnson (2000) subdivided *E. pellita* populations into two species. The *E. pellita* proper was confined to Australian populations around Cardwell–Cairns–Helenvale, Queensland provenance. The remaining populations from Cape York, Australia to New Guinea, including Papua New Guinea and Irian Jaya, Indonesia, were allocated to a new species, *E. biterranea*, distinguishable from *E. pellita* by its smaller buds, fruits and leaves. There has been molecular evidence of a strong genetic structure separating Queensland from Cape York and New Guinea provenances (House & Bell 1996, Le 2009); however, it is debatable. Almost all subsequent scientific publications considered populations from Queensland, Cape York and New Guinea to be *E. pellita* (Boland et al. 2006, Brawner et al. 2013). Therefore, the designation of *E. pellita* is maintained to all Australian and New Guinea provenances.

Published reports on differences between *E. pellita* provenances gave conflicting results. In general, New Guinea provenances were found to have better growth and form than Queensland and especially Cape York in lowland wet tropical conditions with little or no dry season (Harwood et al. 1997, Brawner et al. 2013). On drier open forests or savannas, differences between Australia and New Guinea provenances were less apparent, although other species such as *E. urophylla* and *E. urograndis* hybrids were more productive (Pegg & Wang 1994, Pinyopusarerk et al. 1996).

The objective of the current study was to compare the genetic merit of these various *E. pellita* sources in the wet and hot conditions of Orinoquia region in Colombia and obtain key genetic parameters for growth and stem straightness. The information is important to support the breeding efforts of the species in Colombia.

## MATERIALS AND METHODS

### Provenance/progeny trial

The material represented in the trial was divided into two groups. The first group included 13 open pollinated families of New Guinea origin and four bulked provenance lots from

Queensland (Table 1). The New Guinea families were collected ex-situ from an arboretum established by Refocosta in 1990 (Nieto & Gasca 2008, Refocosta 2010). The arboretum included several species of potential viability in tropical conditions of which *E. pellita* was represented by two New Guinea provenances, namely, Oriomo Plateau in the west (CSIRO seedlot 18199/Serisa Village) and Bupul-Muting in the Merauke region of Irian Jaya, Indonesia (CSIRO seedlot 17854). The 13 open-pollinated families were collected from phenotypically outstanding trees in the two *E. pellita* provenance plots of the arboretum, hence expected to present some degree of selection and better adaptation to local conditions. Although mothers of these families were unambiguously allocated to one of the two New Guinea provenances, families would have been sired by a pollen mix of unselected neighbouring trees from both seedlots, 18199 and 17854. Twelve of the families were from mother trees that originated from Oriomo Plateau and the remaining from Bupul-Muting. The second group of materials represented in the trial included four provenances from Queensland. Each was based on a bulk of native seeds collected from several trees within a location (Table 1).

## Trial location

The provenance/progeny trial was located near the city of Villanueva in the Colombian district of Casanare, 4° 39' N and 72° 54' W, altitude 420 m above sea level (Figure 1). The site received an annual rainfall of 2500–3000 mm, mainly from May till October, and a short drier period between December and February. Nevertheless, there would be 1–2 months of less than 60 mm rainfall per year. Due to high temperatures throughout the year between 20 and 24 °C and annual average temperature of 24 °C, the site is classified as having Am type climate (Kottek et al. 2006). The soil was described as *Dystric cambisols* (Ustoxic Dystropepts Inceptisols, USDA soil classification). It is derived from heterogeneous alluvial deposits originated from the eastern slopes of cordillera (Robertson 2007). It is well drained, of clay loam texture and is moderately acidic, pH = 5, and has very low natural fertility.

The trial was established in December 2008. Previously the soil was covered with pasture. Prior to plantation, the soil was ripped at an average depth of 50 cm and fertilised with one tonne $ha^{-1}$ of Fosmacal, a local fertiliser with 13% phosphorus (P), 25% calcium (Ca), 7% magnesium (Mg), 0.15% boron (B), 0.23% zinc (Zn) and 0.1% manganese (Mn). During planting, each tree received a further 150 g of N + P + K + Mg + sulphur fertiliser (13:26:10:3:3). A second fertilisation was applied at 11 months of age, with 200 g $plant^{-1}$ of another N:P:K:Mg fertiliser (15:4:23:4), plus a further 10 g $plant^{-1}$ of Borax. Weeds and ants were carefully controlled throughout the experiment.

**Table 1** Provenances represented in the trial

| CSIRO seedlot numbers | Locality | Provenance / Family | Latitude | Longitude | Altitude m asl |
|---|---|---|---|---|---|
| Queensland (Australia) | | | | | |
| 18313 | Starcke Station Hopevale | Bulked (30*) | 15° 05' S | 145° 12' E | 30 |
| 13826 | Bloomfield | Bulked (12) | 16° 04' S | 145° 19' E | 200 |
| 18750 | Wonga | Bulked (15) | 16° 16' S | 145° 22' E | 15 |
| 14916 | North of Kuranda | Bulked (15) | 16° 49' S | 145° 38' E | 400 |
| Papua New Guinea | | | | | |
| 17854 | Bupul-Muting (IND) | 1 (17**) | 7° 21' S | 140° 36' E | 40 |
| 18199 | Serisa Village (PNG) | 12 (39) | 8° 36' S | 141° 26' E | 45 |

* Putative number of native female parents contributing to the bulked seedlot, ** putative number of native male parents contributing to the open-pollinated families; asl = above sea level

## Experimental layout

The provenance/progeny trial was established as a randomised complete block design with 18 blocks. Each family or provenance was represented in each block by a single six-tree row plot. The progeny trial was established as a regular 36 m × 51 m rectangular grid, with trees established on a 3 m × 2.5 m spacing, with smaller spacing set along rows.

## Measurements and statistical analysis

Trees were measured annually from ages one to four years for height and diameter at breast height and at age 5 years for stem straightness in a relative scale, 1 = worse and 6 = best. The assessors tried to assign trees to each class according to their expected score, i.e. 2% in classes 1 and 6, 15% in classes 2 and 5 and the remaining in classes 3 and 4. Volume per tree, under the bark, was approximated using the following local volume equation:

$$V = 0.000051265D^{1.8753} H^{0.9888}$$

where V = individual tree volume in $m^3$ and D and H = diameter at breast height in cm and height in m respectively. This equation has been previously fitted for young *E. pellita* trees growing in the same region.

The provenance/progeny trial was analysed based on the following linear model in matrix notation:

$$y = Xb + Z_1 f + Z_2 p + e$$

where y = vector of observations, b = vector of fixed effects of blocks and provenances with its corresponding design matrix X, f = vector of random family effects with its design matrix $Z_1$, p = vector of random plots effects with design matrix $Z_2$ and e = vector of residual effects. Solutions for fixed and random effect were obtained by solving the mixed model equations (Henderson 1984). Given the regular grid structure of the trial, it was possible to fit a spatial analysis framework. Residual effects (e) were separated into a spatially dependent term (ξ) and spatially independent (η) error term (Dutkowski et al. 2002). The covariance structure for these error components, denoted as matrix R, assumed an independent first-order autoregressive pattern for rows and columns which can be represented as:

$$R = I\sigma_e^2 = \sigma_\xi^2[AR1(\rho_{col}) \otimes AR1(\rho_{row})] + I\sigma_\eta^2$$

where $\sigma_\xi^2$ = spatial residual variance, $\sigma_\eta^2$ = independent residual variance called nugget effect according to spatial statistics literature, I = identity matrix and ⊗ = Kronecker product. In the analysis, the independent error term ($\sigma_\eta^2$), was never found to be significant and it was dropped from the final model. The AR1(ρ) represents a first-order autoregressive correlation matrix with ρ, the autocorrelation parameter which independently fits for rows and columns. This matrix, for the simplified case of ordered spatial coordinates of size n, has the form:

$$AR1(\rho) = \begin{bmatrix} 1 & \rho & \rho^2 & \cdots & \rho^n \\ \rho & 1 & \rho & \cdots & \vdots \\ \rho^2 & \rho & 1 & \cdots & \vdots \\ \vdots & \vdots & \ddots & \ddots & \vdots \\ \rho^n & \cdots & \cdots & \cdots & 1 \end{bmatrix}$$

The model also fitted a separate residual term for observations from four Australian provenances. Provenance residual variance included all genetic and environmental variance whereas the open pollinated families from New Guinea had ¾ additive variance plus environmental effects. Multivariate analysis between traits was based on the same linear model as the univariate analysis presented above although no spatial effects were fitted. Restricted maximum likelihood (REML) estimates of variance and co variance components were obtained using ASREML software (Release 2.0, 2006).

The narrow-sense heritability and correlations was calculated from variance and covariance components derived from New Guinean families. The heritability ($h^2$) assumed an intra-class correlation between open-pollinated family members, r = 1/3.3, to account for possible selfing among open-pollinated sibs (Squillace 1974):

$$h^2 = \frac{3.3\sigma_f^2}{\sigma_f^2 + \sigma_\rho^2 + \sigma_\xi^2}$$

where $\sigma_f^2$ , $\sigma_\rho^2$ and $\sigma_\xi^2$ are the family, plot and residual variances respectively. Genetic correlations were estimated based on the standard formula:

$$r = \frac{cov_{ij}}{\sigma_i \sigma_j}$$

$cov_{ij}$ = the family covariance between traits i and j and $\sigma_i$ and $\sigma_j$ = corresponding standard deviation. Standard errors for heritability and correlations were based on Delta method as derived by ASREML (Lynch & Walsh 1998).

## RESULTS

### Provenance effects

Mean individual tree diameter, height and volume at age 4 years were 9.8 cm, 13.7 m and 0.06 $m^3$ respectively. Survival was high, from 91% at age 2 years to 88% at 4 years. Families from New Guinea had significantly better height, diameter and form compared with Queensland provenances (Table 2). Among the Australian provenances, Bloomfield and Kuranda clearly outperformed Wonga and Hopevale for both growth and form.

### Variance components and genetic parameters

Although spatial analysis improved the fitness of the model, the impact on variance component estimates was minor. Significant spatial correlation effects were found for diameter at later ages and for height at age 1 year. On the other hand, stem straightness measured at age 5 years had no significant spatial autocorrelation. Block effects were not significant. Both the results indicated microsite conditions to be highly homogeneous.

The most striking results were the low estimates of heritability, especially after age two years for both growth and stem straightness with $h^2$ being consistently less than 0.05. Heritability estimates were higher at age 1 year, i.e 0.17 for diameter and 0.10 for height. Plot effects were initially significant for height and diameter but later became non-significant. Overall, they were of small magnitude accounting for less than 6% of total variance (Table 3).

Spatial analysis provided interesting insight into the possible interactions between neighbouring tree phenotypes. The autocorrelations (ρ) changed from slightly positive to null values at age 1 year indicating a slight microsite spatial similarity to an increasingly negative estimate at later ages especially for diameter. Negative autocorrelations were an indication of competition among neighbouring trees. Autocorrelation was clearly more negative between rows than columns, which was consistent with the layout of the family/provenance plots of six trees along the row and the shorter inter-row distances.

Genetic correlation between growth measurements at different ages is shown in Table 4. Growth response was consistent across ages. Genetic correlation between ages 1 and 4 years for diameter was 0.80 and for height was 0.94. Correlations improved as age differences reduced.

Genetic correlations between height and diameter at any given age were consistently high,

**Table 2** Least square means for provenance effects and corresponding F-test and standard errors of differences for height (H) and diameter (D), ages 1–4 years, and form, 1–6 scale at age 5 years

| Provenance | D1 | D2 | D3 | D4 | H1 | H2 | H3 | H4 | F5 |
|---|---|---|---|---|---|---|---|---|---|
| Queensland, Australia | | | | | | | | | |
| Daintree (13826) | 5.08 | 8.32 | 9.92 | 10.87 | 5.53 | 9.43 | 12.29 | 14.82 | 2.57 |
| Hopevale (18313) | 3.85 | 6.23 | 6.83 | 7.13 | 4.80 | 7.89 | 9.77 | 11.27 | 1.94 |
| Kuranda (14916) | 4.72 | 7.99 | 9.45 | 10.26 | 5.44 | 9.16 | 12.06 | 13.91 | 2.95 |
| Wonga (18750) | 4.08 | 7.16 | 8.14 | 8.68 | 4.79 | 8.46 | 10.70 | 12.51 | 2.26 |
| New Guinea | | | | | | | | | |
| (PNG and IND) | 5.29 | 8.83 | 10.49 | 11.83 | 5.66 | 9.52 | 13.04 | 15.80 | 3.63 |
| Fprov | 10.22 | 21.73 | 26.51 | 32.34 | 5.56 | 13.24 | 23.79 | 31.20 | 39.86 |
| SED | 0.32 | 0.38 | 0.48 | 0.567 | 0.276 | 0.30 | 0.46 | 0.57 | 0.199 |

$r_G$ = 0.84. Correlations between diameter, at age 4 years and stem straightness at age 5 years was strongly positive, $r_G$ = 0.61 ± 0.41, whereas the genetic correlation between height and stem straightness was null, $r_G$=0.00 ± 0.56. The large standard errors associated with these estimates were a consequence of low heritability of traits.

## DISCUSSION

Field testing of New Guinea provenances was relatively recent and seed sources available were insufficient to be able to sample all possible genetic diversity of the species within Papua New Guinea and Irian Jaya (Harwood 1998, Vercoe and McDonald 1991). The New Guinea sources were represented by two locations and the families were collected ex-situ from phenotypically outstanding trees in a local arboretum. Differences may therefore confound true provenance effects with subsequent local selective advantage of New Guinea families. Nevertheless, the superiority of New Guinea families over the four Queensland locations amounted to 32% in diameter and 22% in height. Differences in stem straightness were also highly significant. These differences were large enough to suggest that New Guinea populations in Keru and Bupul-Muting were better suited to the wet and hot local conditions of Colombia. Most New Guinea locations were superior to Queensland provenances in the lowland tropics with a short dry season, as in Malaysia or Sumatra. Differences between the two provenances seem to be less apparent in savanna or higher altitude conditions (Harwood et al. 1997, Harwood 1998, Brawner et al. 2013).

Among the four Australian provenances tested, Bloomfield and Kuranda had significantly

**Table 3** Trends over time in family, plot and residual variance components, the autoregressive correlations between rows ($AR_{row}$) and columns ($AR_{col}$) and heritability estimates ($h^2$), with their associated standard errors in parentheses for height, diameter and stem straightness

| Age | Family | Plot | Residual | $AR_{row}$ | $AR_{col}$ | $h^2$(se) |
|---|---|---|---|---|---|---|
| Height | | | | | | |
| 1 | 0.115 | 0.336 | 2.550 | 0.01 | 0.06 | 0.13 (0.07) |
| 2 | 0.094 | 0.236 | 4.071 | -0.05 | 0.00 | 0.07 (0.04) |
| 3 | 0.182 | 0.634 | 9.097 | -0.06 | 0.00 | 0.06 (0.04) |
| 4 | 0.205 | 0.979 | 14.582 | -0.06 | 0.00 | 0.04 (0.03) |
| Diameter | | | | | | |
| 1 | 0.118 | 0.453 | 3.158 | -0.03 | 0.03 | 0.10 (0.06) |
| 2 | 0.095 | 0.340 | 7.680 | -0.12 | -0.03 | 0.04 (0.03) |
| 3 | 0.128 | 0.483 | 12.78 | -0.12 | -0.05 | 0.03 (0.03) |
| 4 | 0.173 | 0.818 | 17.72 | -0.16 | -0.07 | 0.03 (0.03) |
| Form | | | | | | |
| 5 | 0.134 | 0.096 | 1.626 | 0.02 | -0.01 | 0.06 (0.03) |

Experimental design included six tree linear plots along rows

**Table 4** Genetic correlations at different ages for diameter (above diagonal) and height (below diagonal)

| Age | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| 1 | | 0.98 | 0.90 | 0.80 |
| 2 | 1.00 | | 0.97 | 0.87 |
| 3 | 0.97 | 1.00 | | 0.98 |
| 4 | 0.94 | 1.00 | 0.98 | |

Standard errors ranged between 0.01 and 0.03

better growth and form. Kuranda has been listed as one of the best Australian provenances (Harwood 1998, Luo et al. 2006, Brawner et al. 2013). On the opposite end, Hopevale/Starcke Station had very poor growth and form (Luo et al. 2006). Hopevale/Starcke Station is located at Queensland *E. pellita* distribution range and considered part of the core *E. pellita* population. However, some specimens of *E. biterreana* akin to Cape York populations were co-occurring here, known to be of poor growth (Harwood 1998, Hill & Johnson 2000). Hopevale material presented in the trial may have included some of these poorer Cape York type germplasm. The two best Australian provenances in the trial, Bloomfield and Kuranda, were at higher altitudes, 200–400 m, whereas Hopevale and Wonga were coastal locations. Altitudinal gradients in growth rate were common in several eucalypt species, e.g, *E. globulus* (Foster et al. 2007) and may be relevant to these Australian and New Guinean *E. pellita* populations. Nevertheless, these four Australian provenances were geographically close to each other, with a maximum of 120 km separating them.

It is debatable whether the marked superiority of the restricted New Guinea provenances would survive in drier and more seasonal conditions of Orinoquia savannas further east, where most of the future plantations are likely to develop. Harwood (1998) reported that in drier tropical savannas, several Queensland provenances outperformed New Guinea material. However, moving from the wet evergreen forest conditions towards savanna, other species such as *E. urophylla* and *E. urograndis* outperformed *E. pellita* in growth, as found in Brazilian Cerrado and African savanna (Bernardo et al. 1997, Gwaze et al. 2000). In wet climates, *E. pellita* is the species of choice due to its resistance to a range of leaf fungi and pathogens known to cause *E. urophylla* and *E. urograndis* plantations to fail (Bouvet & Vigneron 1995, Harwood 1998). Even if pure *E. pellita* proves to be less productive than other species and hybrids, it represents a useful germplasm for interspecific hybridisation for increased resistance. Its ability to produce viable hybrids with both *E. urophylla* and *E. grandis* is an important breeding option when conditions become too wet. Such schemes have been implemented in Amazonia, Sumatra and Congo (Gonçalves et al. 2013, Hardiyanto & Tridasa 2000, Vigneron et al. 2000) and could be a valuable option in Colombia.

Heritability was based on restricted number of families from two New Guinea populations. They were lower ($h^2 < 0.05$) than published estimates for *E. pellita* which ranged between 0.08 and 0.33 for growth (Brawner et al. 2013, Hardiyanto 2003). Genetic variation captured in the early Refocosta introduction of the species was too low, since the arboretum had only two sources and 12 of 13 families came from Serisa Village, Papua New Guinea and the other family, from Bupul-Muting, Irian Jaya. House and Bell (1996) found this location to have high levels of selfing, > 50%, and low genetic diversity, thus the current seed productions available in Colombia are likely to be of low genetic diversity. Trees from the two best Queensland provenances could broaden the genetic diversity of *E. pellita* breeding population in Colombia.

Strong genetic correlation across ages, for both diameter and height, was typical in most fast-growing eucalypts and indicated selection could be effective as early as at age 1 year. Height and diameter were strongly correlated at all ages. Stem straightness was strongly related with diameter, both at family and provenance level. However, the same was not found between height and stem straightness which had zero genetic correlation.

The results from this study were based on a single trial location and included a limited range of provenances. The species was well adapted to wetter conditions of Orinoquia in Colombia. Sources from Serisa Village in Papua New Guinea seemed better adapted than Queensland. Although some concern remained that the early introduction to Colombia may have had too narrow genetic basis, the population established by Refocosta in the Orinoquia seemed to be a valuable genetic resource for pure species deployment or future hybridisation programmes with other species.

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