ORIGINAL ARTICLE

Genetic divergence among slash pine second generation progenies at an early age

Divergência genética entre progênies de segunda geração de Pinus elliottii Engelm. var. elliottii

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Abstract

The objective of this study was to estimate the genetic divergence among slash pine open-pollinated progenies at an early age. Two progeny tests were established in a randomized complete block design, single-tree plots planted in March, 2009, in a 3 x 3.0 m spacing. One test was planted in Ribeirão Branco, São Paulo State, involving 44 progenies in 40 blocks. The other one was planted in Ponta Grossa, Paraná State, with 24 progenies in 32 blocks. Growth and form traits were assessed five years after planting. Genetic divergence was estimated by using the Mahalanobis distance method. Two hierarchical grouping methods were compared: UPGMA and Tocher optimization. Both of these showed similar results and identified five and ten groups, respectively in Ribeirão Branco and Ponta Grossa tests. In order to avoid losses in genetic gain in subsequent generations, crosses should be restricted to individuals belonging to families in divergent groups.

Keywords: *Pinus elliottii* Engelm. var. *elliottii*; Mahalanobis distance; UPGMA; Tocher optimization.

Resumo

O objetivo do estudo foi estimar a divergência genética entre progênies de polinização aberta de *Pinus elliottii* em idade precoce. Dois testes de progênie foram estabelecidos em delineamento de blocos casualizados, uma planta por parcela, plantados em março de 2009, em espaçamento 3 x 3 m. Um teste foi plantado em Ribeirão Branco, São Paulo, envolvendo 44 progênies em 40 blocos. O outro foi plantado em Ponta Grossa, Paraná, com 24 progênies e 32 blocos. Foram avaliados caracteres de crescimento e de forma cinco anos após o plantio. A divergência genética foi avaliada pelo método de Mahalanobis. Dois métodos de agrupamento hierárquico foram comparados: UPGMA e Otimização de Tocher. Ambos mostraram resultados similares e identificaram cinco e dez grupos, respectivamente para os testes de Ribeirão Branco e Ponta Grossa. Com a finalidade de evitar a perda de ganho genético nas gerações subsequentes, cruzamentos deverão ser restritos entre indivíduos de grupos distintos.

Palavras-chave: *Pinus elliottii* Engelm. var. *elliottii*; Distância de Mahalanobis; UPGMA; Otimização de Tocher.

INTRODUCTION

Exotic forest tree species were initially introduced in Brazil as a way to boost the country's economic development, and to offer an alternative to native tree species as sources of timber (Sampaio et al., 2000). Several species from all over the world, with contrasting ecological requirements, were tried by private owners, companies and government agencies in subsequent years. Species from specific regions in the United States, Mexico, Central America, Caribbean Islands, Australia and a few from Asia were most successful and became widely planted in Brazil (Silva et al., 2012) for commercial purposes.

Slash pine (*Pinuselliottii* Engelm. var. *elliottii*) is one of the southern United States yellow pines that have shown great ability to adapt to different environments (United States Department of Agriculture, 2004) and has become an outstanding source of wood and resin products in the Brazilian subtropical region. In spite of a faster growth rate than in its natural range, slash pine commercial stands not always do become an economically attractive investment in Brazil, mostly because of poor stem form, bad branching habits, and poor wood quality in general. Genetic variations in economically important traits are substantial and offer opportunities for increased yield and quality through selection and breeding over generations (Carvalho et al., 2003).

In tree species, the ex situ conservation with provenances and progenies tests is indicated for allowing genetic variability monitoring of related growth and form traits over time and to perform as a base population for breeding programs and seed production for reforestation (Zaruma et al., 2015).

According to Namkoong (1979) a basic program of forest improvement may be basically divided into three stages such as selection of species; selection of provenances within the most adapted and selection of progenies within or from the most adapted origin. The pine improvement program has been focused mainly on paper, cellulose, long fibre, sawn wood and for resin extraction. One of the advantages of pine genetic improvement is the increase of genetic gain rates for growth and form traits, and further the characterization of genetic distance for future improvement (Souza et al., 2016).

Genetic divergence may be estimated based on dialelics analysis; however, this crossing design is costly, especially in forest trees. An alternative method is to measure dissimilarities in morphological and physiological traits among genotypes by using either Mahalanobis or Euclidean generalized distances (Cruz et al., 2004). The estimation of the Mahalanobis distance requires replicated experiments and offers more advantage than the Euclidean distance because it takes into consideration the correlation among traits. Data on distance estimates between offspring pairs can be displayed as a symmetrical matrix where distances can be easily shown as clusters or graphic dispersion. The Mahalanobis distance has been shown to be a suitable means for parental selection (Maluf et al., 1983; Dias & Kageyama, 1997; Machado et al., 2002; Suinaga et al., 2003).

Cluster methods are convenient to separate the initial population of genotypes into groups so that genotypes are more similar within than between groups. Hierarchical and optimization methods are the most commonly used ways to cluster data into groups in plant breeding (Bertan et al., 2006).

In hierarchical methods, offspring are grouped progressively in repeated series, at different levels, so that a dendrogram is drawn with no limit on the number of groups. There are several ways to build cluster structures. One is known as the average distance method (UPGMA) (Cruz et al., 2004). It is based on the average distance between all pairs of offspring.

In optimization methods, groups are formed in ways so that they become mutually specific. For example, in the Tocher method, the basic criterion is to maintain the average distance intra-group always smaller than inter-groups (Rao, 1952; Cruz et al., 2004).

Genetic diversity provides the necessary genetic potential to render populations more resilient to changes in both environmental events such as disease outbreaks and other disasters, and stochastic events in the form of allele losses due to chance (Cui et al., 2001). It is also the basis for advancement in plant breeding. Genetically divergent parents in a segregating population offer a greater probability to generate favourable combinations when new zygotes are formed (Manfio et al., 2012).

In this study, the objective was to estimate the genetic distance among slash pine offspring. Growth and form traits were analysed by multivariate procedures and different clustering methods. The results are expected to provide a guideline for control pollinations in breeding programs for wood production.

MATERIAL AND METHODS

The trials

Forty-four slash pine open pollinated first generation progenies from a seed orchard, established in Colombo, Paraná State, Brazil, were used in this study. This genetic material tested are progenies of free pollination among slash pine ramets in a clonal orchard. These ramets were selected by productivity and stem straightness in commercial plantations established by forest companies in São Paulo and Paraná States. Originally commercial plantings were established with seed introduced from the South and Southeastern United States.

In March 2009, two progeny tests were established: one in Ponta Grossa, Paraná State and the other in Ribeirão Branco, São Paulo State, Brazil (Table 1 and Figure 1).

Table 1. Details of slash pine progeny tests established in Ribeirão Branco, São Paulo State and Ponta Grossa, Paraná State, Brazil.

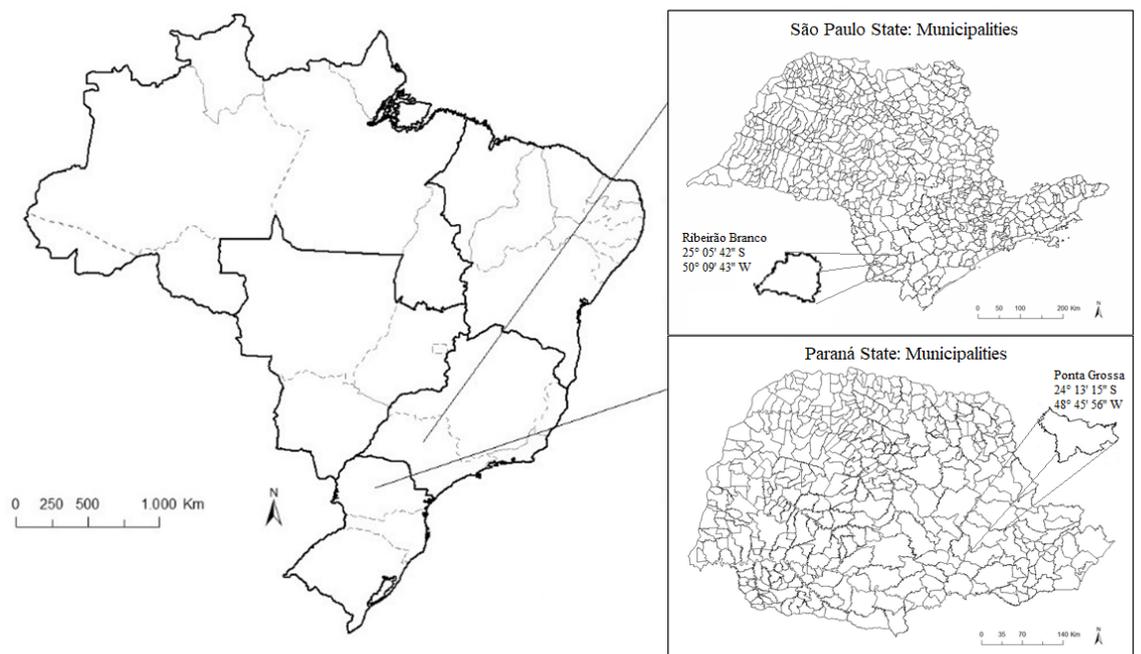|	**Ribeirão Branco**	**Ponta Grossa**
Number of progenies	44	24
Blocks	40	32
Controls	6	-
Spacing	3 x 3 m	3 x 3 m
Latitude	25° 05' 42" S	24° 13' 15" S
Longitude	50° 09' 43" W	48° 45' 56" W
Elevation	969 m	875 m
Rainfall	1,346 mm	1,495 mm
Climate type (Köppen system)	Cfb	Cfb
Annual mean temperature	18 °C	17.5 °C
Soil type	Cambissolo	Cambissolo

Figure 1. Geographic location of Ribeirão Branco, São Paulo State and Ponta Grossa, Paraná State municipalities (Brazil). Source: adapted from Instituto Brasileiro de Geografia e Estatística (2015a, 2015b) map base.

Traits measurement

Assessments of survival, total height (H), diameter at breast height (dbh) and stem quality scores were taken during the five-year period after planting. Total height was measured with a telescoping measurement pole, the stem girth with a tape measure, and survival was assessed by assigning values "1" to living and "0" to dead plants. Stem quality scores were visually assessed as follow (Table 2). Wood volume (VOL, m³) was estimated based on the equation:

$$VOL = \frac{\pi H \left(dbh^2 \right) F}{40000}$$ (1)

Where:
F = stem form factor (0 – 1);

Table 2. Slash pine stem quality scores in Ribeirão Branco, São Paulo State and Ponta Grossa, Paraná State progeny trials.

Trait	Ribeirão Branco		Ponta Grossa	
	Scale	Description	Scale	Description
Stem straightness	1-3	1= most crooked stems, 3= straightest stems	1-5	1= most crooked stems, 5= straightest stems
Branch thickness	1-3	1= thicker, 3= thinner	1-3	1= thicker, 3= thinner
Branch angle	1-3	1< 45º, 2> 45º, 3= approximately 90º	1-3	1< 45º, 2> 45º, 3= approximately 90º
Number of branches	1-7	1= 42-48 branches, 7= 1-6 branches	1-7	1= 17-18 branches, 7= 0-2 branches
Forking	1 and 2	1= absent, 2= present	1 and 2	1= absent, 2= present
Fox tail	1 and 2	1= absent, 2= present	1 and 2	1= absent, 2= present

Estimates of genetic distance

The genetic diversity among offspring was estimated by the Generalized Mahalanobis Distance (D^2) method which is suitable for the analysis of quantitative data considering standard deviation and invariant scale (Cruz et al., 2004) by:

$$D_{ii'}^2 = \delta' \Psi^{-1} \delta \,,$$ (2)

Where,

$D_{ii'}^2$ is the Mahalanobis distance between genotypes i and i',

δ' = [d1, d2, ..., dv]; $d_j = Y_{ij} - Y_{i'j}$,

Ψ is the residual variance and covariance matrices,

Y_{ij} = mean of the ith genotype with respect to the jth variable.

The analysis was performed with the software SELEGEN-REML/BLUP (Resende, 2007), which considers variance matrices and residual covariances between traits, and generates data to build a hierarchical structure dendrogram based on average distance (UPGMA - Unweighted Pair Group Method using Arithmetical Averages). This part of the analysis was performed with the statistical software R, version 3.2.0.

Tocher optimization method (Cruz et al., 2004) was applied to identify homogeneous genotype groups. This method is based on the criterion in which average distances (D^2) are always lower between genotypes within groups (intra-cluster) than between genotypes in different groups (inter-cluster). The maximum distance considered was 100% for both sites and the minimum were 10 and 24.8% in Ribeirão Branco and Ponta Grossa, respectively.

RESULTS AND DISCUSSION

Generalized Mahalanobis distance

Genetic distances among progenies were wider in Ribeirão Branco than in Ponta Grossa. That could be because of the larger number of offspring (44) in that site than in Ponta Grossa (24). The maximum genetic distance observed in Ribeirão Branco was between progenies C-053-1 and C-197, and the minimum was between C-084-2 and C-112-1. In Ponta Grossa, the maximum distance was detected between progenies C-047-1 and C-023-1, and the minimum between progenies C-084-2 and C-025-3 (Table 3).

Genetic distances estimated by the Mahalanobis generalized method in this study were higher than that observed in *Pinus caribaea* var. *caribaea* (Silva et al., 2012; Santos et al., 2016) and *P. caribaea* var. *bahamensis* (Missio et al., 2007). Apart from analyzing different species, this study was based on much younger individuals than in other studies and could be part of the reason for the higher genetic divergence observed.

Table 3. Generalized Mahalanobis Distance (D^2) in percentage relative to the greatest distance between slash pine progenies in Ribeirão Branco, São Paulo State and Ponta Grossa, Paraná State, Brazil.

Progeny	Greater (%)	Progeny	Smaller (%)	Progeny	Progeny	Greater (%)	Progeny	Smaller (%)	Progeny
				Ribeirão Branco					
C-016-2	72.6	C-098-1	23.0	C-013	C-032-1	65.6	C-081-3	28.6	C-025-3
C-082-1	61.6	C-047-1	19.9	C-084-2	C-068-1	59.6	C-159-1	27.2	C-063-2
C-082-1	73.2	C-071-1	18.3	C-032-2	C-053-1	71.8	C-217-1	30.9	C-048-2
C-074-2	65.2	C-010-1	18.6	C-045-1	C-053-1	75.2	C-048-2	24.9	C-059-1
C-082-1	61.3	C-023-1	21.4	C-112-1	C-053-1	65.2	C-272-1	21.3	C-043-3
C-053-1	70.4	C-100-2	23.7	C-001-1	C-053-1	62.0	C-128-2	62.0	C-053-1
C-197	55.1	C-084-2	10.5	C-112-1	C-053-1	65.5	C-032-1	35.8	C-043-3
C-082-1	59,7	C-120-1	59.7	C-082-1	C-063-2	55.8	C-053-1	48.5	C-032-2
C-053-1	69.3	C-036-1	18.7	C-048-2	C-047-2	77.0	C-068-1	33.5	C-043-3
C-053-1	82.5	C-012-3	26.0	C-045-1	C-019-1	60.4	C-063-2	40.3	C-013
C-082-1	67.3	C-151-1	21.5	C-039-1	C-016-2	64.9	C-042-1	24.4	C-013
C-082-1	69.4	C-045-1	23.3	C-189-1	C-218-1	50.5	C-043-3	25.0	C-032-2
C-082-1	70.2	C-112-1	11.6	C-218-1	C-025-3	49.8	C-047-2	25.0	C-218-1
C-053-1	76.9	C-001-1	35.0	C-189-1	C-067-1	49.1	C-039-1	25.0	C-013
C-197	68.3	C-039-2	12.5	C-272-1	C-025-3	64.4	C-067-1	23.0	C-032-2
C-053-1	66.6	C-225	16.9	C-013	C-016-2	55.8	C-218-1	25.2	C-019-1
C-074-2	83.9	C-082-1	46.7	C-059-1	C-016-2	58.7	C-013	31.8	C-059-1
C-197	68.5	C-189-1	25.2	C-048-2	C-025-3	42.8	C-019-1	16.0	C-059-1
C-053-1	74.6	C-083-1	33.2	C-047-2	C-059-1	39.0	C-025-3	33.8	C-016-2
C-197	86.7	C-074-2	40.7	C-272-1	C-016-2	33.7	C-032-2	30.8	C-059-1
C-068-1	65.8	C-228	22.3	C-047-2	C-059-1	25.9	C-016-2		
C-053-1	100	C-197	52.3	C-272-1					

Table 3. Continued...

Progeny	Greater (%)	Progeny	Smaller (%)	Progeny	Progeny	Greater (%)	Progeny	Smaller (%)	Progeny
				Ponta Grossa					
C-047-1	80.1	C-084-2	24.8	C-025-3	C-047-1	96.5	C-019-1	36.8	C-012-3
C-197	95.4	C-025-3	52.1	C-083-1	C-047-1	88.9	C-067-1	44,3	C-217-1
C-019-1	89.6	C-010-1	46.5	C-016-2	C-047-1	67.1	C-012-3	32.5	C-083-1
C-039-2	94.2	C-068-1	48.0	C-032-1	C-047-1	83.0	C-225	62.0	C-228
C-047-1	81.7	C-016-2	34.5	C-012-3	C-189-1	85.6	C-036-1	60.9	C-083-1
C-128-2	85.7	C-272-1	37.1	C-083-1	C-047-1	93.0	C-228	62.0	C-083-1
C-036-1	90.7	C-128-2	53.3	C-083-1	C-047-1	93.0	C-189-1	47.0	C-083-1
C-048-2	86.5	C-032-1	30.1	C-012-3	C-047-1	68.6	C-048-2	47.3	C-083-1
C-217-1	91.4	C-013	47.4	C-067-1	C-047-1	94.5	C-197	70.7	C-217-1
C-189-1	86.3	C-032-2	44.2	C-012-3	C-047-1	75.6	C-083-1	60.6	C-217-1
C-023-1	78.3	C-039-2	14.1	C-225	C-217-1	84.4	C-047-1		
C-047-1	100	C-023-1	33.8	C-036-1					

Ribeirão Branco: maximum: 100% between C-053-1 and C-197, minimum: 10.5% between C-084-2 and C-112-1; Ponta Grossa: maximum: 100% between C-047-1 and C-023-1, minimum: 24.8% between C-084-2 and C-025-3.

According to recommendation by Martins et al. (2002), individuals will be selected for their growth performance and/or genotypic value, combined with the magnitude of their genetic divergence relative to given progenies for controlled crossings. It is expected that crosses C-053-1 x C-197 and C-047-1 x C-023-1 will perform better than other combinations. These pairwise individuals will be assigned to further crosses, especially to determine heterosis effects in quantitative traits.

The magnitude of heterosis effects depends on the presence of directional dominance, epistasis, and allele frequency differences. Since the more genetically divergent individuals tend to generate stronger heterosis effects when crossed, Dias & Kageyama (1997) suggested the inclusion of these individuals in hybridization processes to achieve greater genetic gains. Formation of groups of individuals and families with differing frequencies in alleles affecting target traits has been part of breeding efforts in cross-pollinated species (Betrán et al., 2009).

Hybrid superiority in several traits can arise also due to complementarity among alleles with additive effects. This can result from synergy among independent traits at particular environments where parental species are less adapted than the hybrid (Nicholas, 1987; Sedgley & Griffin, 1989).

As regards the relative importance of traits for families differentiation, the characteristics that presented the highest relative contributions to genetic divergence were: volume at age four in Ribeirão Branco (24%) and dbh at the same age in Ponta Grossa (14%) (Figure 2).
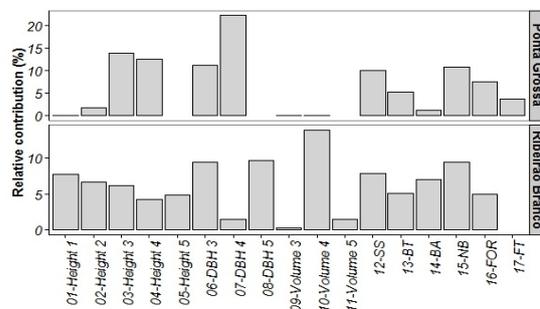

Figure 2. Relative contribution of traits to genetic divergence in dbh (Ponta Grossa) and wood volume (Ribeirão Branco) at four years, based on the generalized Mahalanobis distance. Height 1, Height 2, Height 3, Height 4 and Height 5 = height at one, two, three, four and five years after planting. DBH 3, DBH 4 and DBH 5 = diameter at breast height at three, four and five years after planting. Volume 3, Volume 4 and Volume 5 = wood volume at three, four and five years after planting. SS = stem straightness; BT = branch thickness; BA = branch angle; NB = number of branches; FOR = fork.

According to Pagliarini et al. (2016), who estimated genetic parameters for both sites, both traits were identified as significant, in relation to families evaluation. Furthermore, the publication also noticed the highest narrow-sense individual heritability for them. This indicates that the evaluation of these traits will be important for advanced stages of Slash Pine improvement, with a real possibility to obtain selection gains and contribution to families dissimilarity.

The relative contribution of each trait in determining the magnitude of genetic divergence between progenies is important to identify those that contribute the least to be discarded. This screening will help to reduce time and cost of experiments (Correa & Gonçalves, 2012).

Comparison between clustering methods

Based on the Mahalanobis distance matrix among progenies, a dendrogram was drawn, by using the UPGMA method. Five groups were observed in Ribeirão Branco (Figure 3) and 10 in Ponta Grossa (Figure 4). The estimated coefficient of cophenetic correlation were 0.90 and 0.76 in Ribeirão Branco and Ponta Grossa, respectively, indicating a good fit of distances to graphical representation and the new matrix (Rohlf, 2000). For genetic improvement, the hierarchical method of average distance (UPGMA) is higher than the nearest neighbour and farthest neighbour (Sneath & Sokal, 1973; Dudley, 1994).
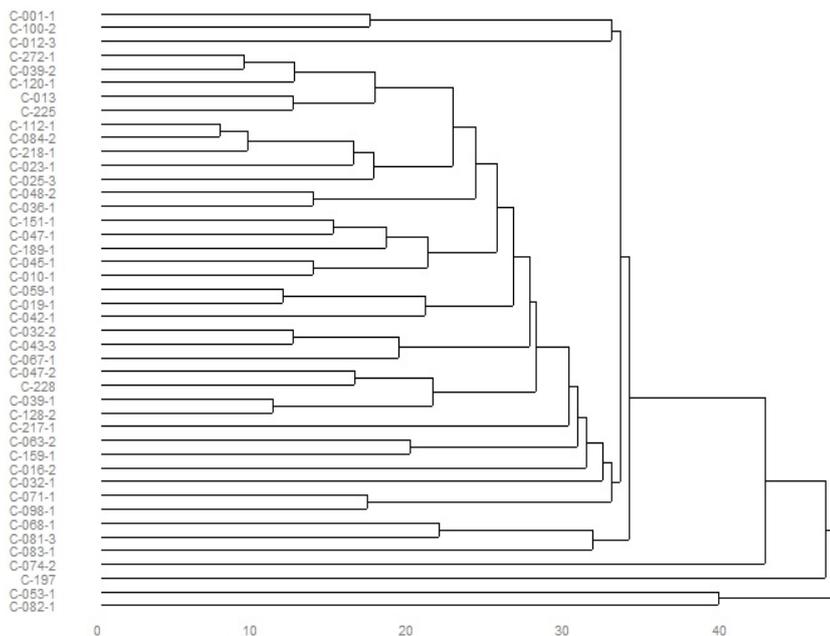

Figure 3. Dendrogram involving 44 slash pine progenies in Ribeirão Branco, São Paulo State, based on the Mahalanobis distance and grouped with UPGMA clustering method. The coefficient of cophenetic value (r) was 0.90.

The Tocher optimization method was effective in separating Ribeirão Branco progenies into five groups (Table 4). Group I included 91% of progenies, while Groups II, III, IV and V included only 2.25% each. Ponta Grossa progenies were separated into 10 groups (Table 4). Group I contained 58.3% of progenies, while group II included 8.3%, and the groups III to X contained 4.2% each. Progenies in Ponta Grossa showed higher genetic divergence than those in Ribeirão Branco and were separated into a larger number of groups. Crosses between more productive individuals from divergent groups should be given priority to increase the likelihood of generating high specific combining ability and heterosis. For example, it is recommended to cross genotype C-197 from group III with C-098-1 from group I to obtain full-sibs. Also, high performing genotypes in Ribeirão Branco should be crossed with high performance genotypes in the Ponta Grossa trial.
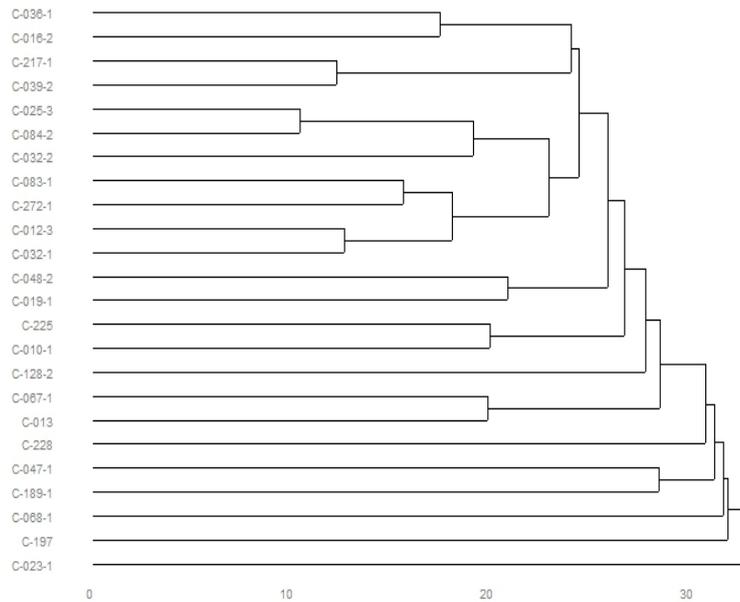
Figure 4. Dendrogram involving 24 slash pine progenies in Ponta Grossa, Paraná State, based on Mahalanobis distance and grouped with UPGMA clustering method. The coefficient of cophenetic value (r) was 0.76

Table 4. Slash pine progeny groups formed by using Tocher optimization method and mean value for height (H), diameter at breast height (dbh), wood volume (VOL) and stem straightness (SS) at age five in Ribeirão Branco and at age four in Ponta Grossa.

Group	Progeny	Total	H (m)	dbh (cm)	VOL (m³tree⁻¹)	SS
	Ribeirão Branco					
I	C-098-1, C-047-1, C-071-1, C-010-1, C-023-1, C-100-2, C-084-2, C-120-1, C-036-1	40	7.31	13.64	0.05	2.11
	C-012-3, C-151-1, C-045-1, C-112-1, C-001-1, C-039-2, C-225, C-189-1, C-083-1					
	C-228, C-081-3, C-159-1, C-217-1, C-048-2, C-272-1					
	C-128-2, C-032-1, C-068-1, C-063-2, C-042-1, C-043-3, C-047-2, C-039-1, C-067-1, C-218-1, C-013, C-019-1					
	C-025-3, C-032-2, C-016-2, C-059-1					
II	C-074-2	1	6.94	12.68	0.04	2.11
III	C-197	1	7.24	13.47	0.05	1.97
IV	C-053-1	1	7.45	13.85	0.05	2.14
V	C-082-1	1	7.13	13.06	0.05	2.31
Total		**44**	**7.25**	**13.34**	**0.05**	**2.15**
	Ponta Grossa					
I	C-084-2, C-025-3, C-016-2, C-272-1, C-032-1, C-032-2	14	5.95	11.32	0.03	2.06
	C-039-2, C-019-1, C-012-3, C-225					
	C-036-1, C-048-2					
	C-083-1, C-217-1					
II	C-013, C-067-1	2	6.02	11.44	0.03	2.10
III	C-010-1	1	6.08	10.80	0.03	2.10
IV	C-189-1	1	6.64	13.19	0.04	2.13

Table 4. Continued...

Group	Progeny	Total	H (m)	dbh (cm)	VOL (m³tree⁻¹)	SS
V	C-128-2	1	6.38	11.85	0.03	2.04
VI	C-228	1	6.13	11.96	0.03	2.05
VII	C-068-1	1	5.78	11.20	0.03	1.95
VIII	C-047-1	1	6.18	11.50	0.03	2.07
IX	C-197	1	6.86	13.97	0.05	2.10
X	C-023-1	1	5.41	10.06	0.03	2.05
Total		**24**	**6.14**	**11.73**	**0.03**	**2.07**

As clustering method tends to keep together genetically uniform progenies within a group and genetically divergent progenies in separate groups, Cruz et al. (2004) recommended crossing only progenies from different groups so that the genetic variability is maintained and losses in gain through selection are avoided.

The highest distance found by the Mahalanobis generalized quantitative distances reveals that there is a greater variability between compared progenies which is confirmed by results obtained by the Tocher grouping. It is possible to note that progenies with greater distance are in different groups, while progenies with smaller distances belong to the same group.

The clustering by using UPGMA method produced a similar result as the formation of groups by using Tocher method. Progenies in Ribeirão Branco belonging to groups II, III, IV and V by Tocher method were about the same as those grouped with UPGMA (Figure 4), except C-225, C-019-1, and C-048-2.

The mean value of each group formed among progenies in Ribeirão Branco with the Tocher method indicates that crosses of individuals in group I with those in group IV are recommended. These groups presented means larger than the total mean and the greatest means among all groups. Among progenies in Ponta Grossa, crosses of individuals in groups IV with those in IX are recommended. In breeding programs, it is desirable to cross individuals that are genetically divergent and with high means so that productive genotypes are combined and complement each other to express the non-additive fraction of the genetic variance (Nascimento et al., 2014). High genetic divergence is essential also for the development of productive intraspecific hybrids. However, when the objective is to recover genes through recurrent crosses, these should involve progenies that are most genetically similar or with low genetic divergence (Moraes, 2001).

CONCLUSIONS

There is genetic divergence among slash pine progenies detected by form and growth traits.

Crossings must be chosen not only by distances between formed groups, but it is necessary to take into account the productivity rank because the most distant individuals/progenies are not always be the most productive.

Clustering of progenies into groups by using UPGMA and the Tocher optimization methods produced similar results.

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