



AENSI Journals

Australian Journal of Basic and Applied Sciences

ISSN:1991-8178

Journal home page: www.ajbasweb.com



Genetic Variability of *Dipteryx alata* Vog. (Fabaceae) in a Provenance and Progeny Trial

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ARTICLE INFO

Article history:

Received 8 August 2014

Received in revised form

12 September 2014

Accepted 25 September 2014

Available online 2 November 2014

Keywords:

Isozymes, plant breeding, Brazilian

Savannah

ABSTRACT

Cerrado is the second largest biome in Brazil and one of the most biodiverse regions in the world, being highlighted as a hotspot for biodiversity conservation. The accelerated pace of deforestation of Cerrado, mostly due to the expansion of agricultural activities, intensifies the process of habitat fragmentation and, consequently, in ecological and genetic aspects of the indigenous species. This work aims to study the genetic variability and reproductive system of *Dipteryx alata* in a provenance and progeny trial. This is a tree species native from Cerrado regions widely used by traditional peoples, provider of food and wood for multiple purposes. The trial consists of 66 families of half-siblings, 25 families coming from extreme west, 25 from the northwest and 16 from the mid-north regions of the state of Minas Gerais in the southeast of Brazil. Isozymes extracted from leaf samples were run in polyacrylamide gel electrophoresis and stained with several enzymatic solutions, among which the best revealing enzymatic systems were chosen for analysis. It can be inferred that *D. alata* has a low divergence among the three provenances analyzed based on the similarity in the allele frequencies of populations, along with similar proportions of genetic equity. It is reported that the history of fragmentation in the Cerrado region of Minas Gerais is relatively recent and because of that we hypothesize that not enough time has elapsed for natural populations of *D. alata* occurring in these localities to express genetic changes. The results showed high genetic variability in the three provenances indicating high potential to be employed in genetic improvement, mainly due to the wide variability within populations. In accordance with previous studies we detected a mixed reproduction system with predominance of outcrossing.

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To Cite This Article: Alvaro A.V. Soares, Alisson M. Santos, Dulcinéia de Carvalho, Sebastião C.S. Rosado., Genetic Variability of *Dipteryx Alata* Vog. (Fabaceae) in a Provenance and Progeny Trial. *Aust. J. Basic & Appl. Sci.*, 8(16): 169-175, 2014

INTRODUCTION

The Cerrado, or Brazilian Savannah, is the second largest biome in Brazil and one of the most biodiverse regions in the world (Mittermeier *et al.*, 2004), being highlighted as a hotspot for biodiversity conservation (Myers *et al.*, 2000). The accelerated pace of deforestation of Cerrado has resulted in abrupt changes at the landscape level. These changes had marked effects on physical, biological and social aspects, which may lead to the loss of yet unknown biological resources that could be exploited sustainably. The increased area for agriculture has effect in the devastation in native vegetation, intensifying the process of fragmentation and, consequently, in ecological and genetic aspects of the indigenous species.

The baru (*Dipteryx alata* Vog.) belongs to the family Fabaceae and the subfamily Papilionoideae. It is a tree species of high potential due to its multiple uses, range of occurrence and relevant economics, in addition to its good silvicultural features. This species is widely used by traditional peoples, providing food, since its fruits have high calorific and protein value. It presents straight trunk and high density wood ranging from 0.85 to 1.10 g cm⁻³. These characteristics, combined with a high resistance to decay and attack by xilophagus organisms (Lorenzi, 2002; Carvalho, 1994; Sano *et al.*, 2004) make it well suited for use as poles, fence posts, railway sleepers and in construction.

The aim of this study was to quantify the genetic variability and to investigate the mating system of this species in a provenance and progeny trial in order to subsidize research on the genetic improvement of the species.

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MATERIALS AND METHODS

Characteristics of the study area:

The study was conducted in Brasilândia de Minas, Minas Gerais State, southeast of Brazil, in an 11-year old combined test of provenance/progeny. The geographical coordinates are 17°02'S 45°50'W and altitude of 575m. The climate type is Köppen Aw, maximum and minimum temperatures of 18°C and 26°C, respectively, and average annual rainfall of 1438mm.

The test is part of a project of the Federal University of Lavras in partnership with the Foundation for Research Support of Minas Gerais (FAPEMIG). It aims to establish parameters for the genetic improvement of *Dipteryx alata* in order to recommend it for crops and agroforestry, and to allow the choice of genetic materials adapted and more productive, contributing to sustainability and food security of rural communities and region traditional peoples of the region besides favoring an increase in family income. The experiment consists of 66 families of half-siblings, 25 families come from Capinópolis, 25 from Brasilândia de Minas and 16 from Jequitaí, located respectively in the extreme west, northwest and mid-north of Minas Gerais, which correspond to a wide range of the natural occurrence of this species in the state.

Sampling and electrophoresis procedures:

The genetic analyses were performed in samples of 10 families per provenance and 10 individuals per family, totaling 300 individuals.

The enzyme extraction was done in 200 mg of leaf tissue and 1 mL of extraction solution was added as established by Alfenas (1998). Previously a test of enzymatic systems was carried out, choosing those that best ensured the integrity of the enzymes. Insoluble PVP was added to each sample, which had been macerated with a clean cooled kit of pestle and mortar. Subsequently, the extracts were centrifuged at 12,000 rpm at 4°C for 5 minutes. To perform the electrophoretic runs, 30mL of supernatant were applied in the gels. Polyacrylamide gel was made according to specifications detailed in Alfenas (1998). The electrophoresis was performed in a vertical tank with constant amperage of 20 mA per gel for duration of three hours. After running the gels, they were immersed in 100mL of the previously selected revealing solution.

Processing and data analysis:

The data processing was realized by using with the software UPGMA (Miller, 1997) to calculate allele frequencies, GDA (Lewis and Zaykin, 2000) to estimating diversity indices and MLTR (Ritland, 1997) for the reproductive system.

The allelic frequencies describe the variation for one locus. They were obtained by direct counting of the number of alleles per locus divided by the total number of alleles at locus: $i_j = n_{ij} / n_j$, where: i_j = frequency of allele i in population j ; n_{ij} = number of occurrences of allele i in population j , n_j = total number of alleles sampled in population j .

Indices of genetic diversity:

From the allele frequencies, the following genetic diversity indices were obtained: mean observed heterozygosity (\hat{H}_o), mean expected heterozygosity (\hat{H}_e) according to Hardy-Weinberg Equilibrium, the average number of alleles per locus (A) and percentage of polymorphic loci (P).

Genetic structure of populations:

The study of genetic structure among and within populations was obtained by three criteria: F statistics of Wright, coancestry coefficient of Cockerham, and decomposition of the total heterozygosity into components between and within populations.

Reproductive System:

Models of random mating, Ritland & Jain (1981) mixed mating and correlated matings (Ritland, 1989) were used for the analysis of the reproductive system of *D. alata*.

The analysis of the reproductive system followed the pattern of mix crossing of Ritland & Jain (1981). In this, the following parameters were estimated: multilocus outcrossing rate (\hat{t}_m) by maximum likelihood method, unilocus outcrossings rate (\hat{t}_s), outcrossing rate among relatives ($\hat{t}_m - \hat{t}_s$), correlation of selfing between two siblings (\hat{r}_s), the paternity correlation between two siblings (\hat{r}_p) and the proportions of selfing ($p_s = 1 - \hat{t}_m$), half-siblings ($P_{HS} = \hat{t}_m \cdot (1 - \hat{r}_p)$) and full sibs ($P_{FS} = \hat{r}_p - \hat{t}_m$).

Bootstrap sampling procedure was used to estimate the standard error of the mean for all parameters, the software used the bootstrap sampling procedure with 1000 resamplings as Vencovsky *et al.* (1997).

RESULTS AND DISCUSSION

Enzyme systems:

Twenty enzyme systems were tested and twelve out of them were selected, namely: acid phosphatase (ACP), alfa-esterase (α -EST), beta-esterase (β -EST), glutamic oxaloacetic transaminase (GOT), glutamate dehydrogenase (GTDH), glucose-6-phosphate dehydrogenase (G6PDH), malate dehydrogenase (MDH), peroxidase (PO), sorbitol dehydrogenase (SDH), superoxide dismutase (SOD) and phosphoglucose isomerase (PGI) and phosphoglucomutase (PGM). The selection criterion of enzyme systems was the highest number of loci and quality of revealing.

In studies of genetic diversity carried out by isoenzymes, it is recommended a minimum of ten polymorphic loci (Berg & Hamrick, 1997). This was achieved using five systems, namely: PO, with two polymorphic loci, SOD and SDH with two polymorphic loci and one monomorphic, β -EST with three polymorphic loci, and α -EST with four polymorphic loci. All systems showed loci with the segregation of two alleles.

Allele frequencies:

The estimates of genetic variability within and among populations were obtained by allele frequency of 30 alleles distributed in fifteen loci (Table 1). The highest values of allele frequencies were obtained in the first allele for most loci in three provenances (13 loci in Capinópolis and Jequitaiá and 12 in Brasilândia de Minas). The other loci had similar frequencies of alleles 1 and 2 with the exception of β -EST3 locus, in which the frequency of the second allele (0.634) was higher than the first (0.365). Only the loci SDH3 and SOD3 provided equal frequencies for both alleles in the three populations.

Regarding genetic equity, which is characterized by low amplitude of variation of frequencies between two alleles, a locus is in equity when the frequencies of its alleles are between 0.35 and 0.65. This feature is an indicator of genetic diversity, showing that populations may be less susceptible to fixation and loss of alleles when subjected to disturbances (Frankel *et al.*, 1995). Overall 66.67% of the loci evaluated exhibited alleles in equity. Analyzing separately by provenance, these values are not considerably different, as Capinópolis, Jequitaiá and Brasilândia de Minas presented, respectively, 73.3%, 60% and 66.67% of loci in genetic equity.

Provenances had high frequency alleles, i.e. greater than 0.650. In total, 15 alleles were found at high frequency, four in Capinópolis, six in Jequitaiá and six in Brasilândia de Minas. The most frequent alleles were the α -EST (allele 1 = 0.913) and SOD1 (allele 1 = 0.808) Brasilândia of Minas and α -EST (allele 1 = 0.831) of Jequitaiá.

In general, the allele frequencies among the three provenances were similar and fixed alleles were not observed. However, some had high frequencies, for example allele 1 of α -EST4 locus (0.913) and allele 1 of SOD1 (0.808) from Brasilândia de Minas, and allele 1 of α -EST4 locus (0.831) from Jequitaiá.

This result is probably due to the occurrence of recent forest fragmentation. Although the analysis was performed on progenies, the indicator events of disturbance in tree species are slow, especially given the long cycles of reproduction. It can be inferred that this species has a low divergence among the three provenances analyzed based on the similarity in the allele frequencies of populations, along with similar proportions of genetic equity.

Indices of genetic diversity:

The genetic diversity indices were estimated based on the allele frequencies obtained. Using the rate of 99% as a criterion for the most common allele, we obtained a percentage of 100% polymorphic loci. The number of alleles per locus found for each of the progenies (\hat{A}) was equal to 2.0.

The average expected (\hat{H}_e) and observed (\hat{H}_o) heterozygosities ranged from 0.434 to 0.468 and from 0.639 to 0.650, respectively. These values are in accordance with other studies of tree species, especially in the Cerrado biome. Moraes *et al.* (2005) found values of \hat{H}_e ranging from 0.333 to 0.511 and 0.317 to 0.408 for \hat{H}_e in *Myracrodruon urundeuva*. f. Souza and Carvalho (2005) observed values of \hat{H}_o from 0.492 to 0.550 and of \hat{H}_e from 0.413 to 0.440 for *Stryphnodendron adstringens*. Gonçalves (2010) studying *Dimorphandra mollis*, found values of \hat{H}_o and \hat{H}_e in the range of 0.449 to 0.494 and 0.459 to 0.470, respectively.

Values of \hat{H}_o higher than \hat{H}_e (Table 2) generated a negative fixation index for the three provenances, a fact that shows an excess of heterozygotes in relation to Hardy-Weinberg equilibrium, except for the provenance Brasilândia de Minas. This result was not significant but its value indicates the same tendency in the other provenances. High values of heterozygosity, as the observed in this study, suggest the existence of selection mechanisms acting in favor of heterozygotes.

Table 1: Allele frequencies and sample size (n) in 15 allozyme loci in three provenance of *Dipteryx alata* Vog.

Locus	Allele	Provenance			Mean
		Capinópolis	Jequitaiá	Brasilândia de Minas	
PO1	1	0.629	0.695	0.612	0.644
	2	0.371	0.304	0.387	0.355
	n	124	97	98	319
PO2	1	0.58	0.621	0.663	0.618
	2	0.419	0.378	0.336	0.381
	n	124	99	98	321
SOD1	1	0.68	0.67	0.808	0.717
	2	0.319	0.33	0.191	0.283
	n	119	100	99	318
SOD2	1	0.554	0.53	0.505	0.531
	2	0.445	0.47	0.495	0.468
	n	120	100	100	320
SOD3	1	0.500	0.500	0.500	0.500
	2	0.500	0.500	0.500	0.500
	n	122	100	100	322
SDH1	1	0.571	0.51	0.51	0.533
	2	0.428	0.489	0.489	0.499
	n	119	97	95	311
SDH2	1	0.691	0.684	0.755	0.708
	2	0.308	0.315	0.244	0.291
	n	123	95	98	316
SDH3	1	0.500	0.500	0.500	0.500
	2	0.500	0.500	0.500	0.500
	n	124	99	99	322
β -EST 1	1	0.62	0.527	0.500	0.555
	2	0.379	0.472	0.500	0.444
	n	120	92	92	304
β -EST 2	1	0.611	0.725	0.747	0.699
	2	0.388	0.275	0.252	0.300
	n	81	100	97	278
β -EST 3	1	0.686	0.563	0.365	0.547
	2	0.313	0.436	0.634	0.453
	n	110	95	93	298
α -EST 1	1	0.627	0.582	0.622	0.612
	2	0.372	0.417	0.378	0.388
	n	98	79	82	259
α -EST 2	1	0.642	0.678	0.707	0.674
	2	0.571	0.321	0.292	0.325
	n	119	98	99	316
α -EST 3	1	0.557	0.543	0.425	0.516
	2	0.443	0.456	0.574	0.483
	n	114	81	74	269
α -EST 4	1	0.737	0.831	0.913	0.827
	2	0.262	0.168	0.086	0.172
	n	97	92	98	287

Table 2: Genetic diversity indices in three populations of *Dipteryx alata* Vog., based on fifteen loci and five enzymatic systems.

Indices	Provenances		
	Capinópolis	Jequitaiá	Brasilândia de Minas
\hat{A}	2	2	2
$P_{0.05}$	100	100	100
\hat{H}_o	0.6497(0.0327)	0.6944(0.0600)	0.6388(0.0960)
\hat{H}_e	0.4676(0.1981)	0.4594(0.2024)	0.4339(0.2718)
\hat{f}	-0.3918* [-0.7509; -0.0327]	-0.5158* [-0.7017; -0.0819]	-0.4758 [-0.7969; 0.0133]
N	114.2666	94.9333	94.8000

() = standard error; [] = confidence interval; * = significant at 5%

Genetic structure:

Table 3 presents the coancestry coefficient of Cockerham estimated (Cockerham 1969; Vencovsky, 1992) for the three provenances of *D. alata*. The inbreeding coefficients within provenances and overall were negative and significant at 5%. This result shows no inbreeding detected in neither observations levels, and an excess of heterozygotes.

Table 3: Coefficient of endogamy estimates within provenance (\hat{f}), for the group of provenances (\hat{F}) and estimates of the genetic divergence among populations ($\hat{\theta}_p$) in a provenance and progeny trial of *Dipteryx alata* Vog.

Locus	\hat{f}	\hat{F}	$\hat{\theta}_p$
PO1	-0,488	-0,479	0,006
PO2	-0,209	-0,205	0,004
SOD1	-0,259	-0,228	0,024
SOD2	-0,884	-0,881	0,002
SOD3	-1,000	-1,000	0,000
SDH1	-0,579	-0,573	0,003
SDH2	-0,398	-0,392	0,004
SDH3	-1,000	-1,000	0,000
β -EST1	-0,587	-0,563	0,015
β -EST2	-0,256	-0,231	0,019
β -EST3	0,131	0,215	0,098
α -EST1	-0,535	-0,535	-0,000
α -EST2	-0,079	-0,078	0,000
α -EST3	-0,292	-0,272	0,015
α -EST4	-0,072	-0,019	0,050
Mean	-0,457*	-0,435*	0,015*
	[-0,290; -0,626]	[-0,254; -0,6129]	[0,030; 0,051]

[] = confidence interval; * = significant at 5%

A low but significant value of genetic divergence among populations (0.015) was obtained, indicating that 1.55% of the genetic variation of this test is among the provenances, therefore, 98.5% of the variation lies within the provenances. Most forest species present, according to Carvalho and Oliveira (2005), genetic divergence among populations of less than 5%, with values usually around 3%. Some species of occurrence in Cerrado exhibit the same tendency, for example: *Caryocar brasiliensis* (0.020), *Dimorphandra mollis* (0.025) and *Machaerium villosum* (0.061) (Melo Júnior *et al.* 2004; Gonçalves, 2010; Botrel *et al.*, 2004, respectively). Jaeger (2007) in a study of *Xylopia emarginata* observed a value of genetic divergence of 0.083 and presents a review of studies of several tropical tree species that corroborates the prevalence of low divergence among populations.

In terms of landscape features, the population of Brasilândia de Minas occurs in a region where there is a predominance of monoculture of *Eucalyptus spp.* The trees located in Capinópolis are mostly isolated in pastures and soybean fields. In Jequitaiá, the landscape consists of fragments of Cerrado *sensu stricto*, presenting also moderately hilly relief and agricultural system characterized mostly by family farms, which resulted in a lower degree of human disturbance.

Cerrado areas, especially the regions of North and West of Minas, the latter also known as Minas Triangle, have a recent history of conversion to monocultures such as soybean, *Eucalyptus* and sugar cane (Micheoloto and Vargas, 2008; Monsoon and Martins, 2008). Probably due to this recent fragmentation, not enough time has elapsed for natural populations of *D. alata* occurring in these localities to express genetic changes. We emphasize the long period of growth and reproduction characteristic of tree species.

Reproductive System:

The high values of multilocus outcrossing rates (Table 4) show that *D. alata* has mixed reproduction system predominantly by crossing. Moreover, these values are above average when compared to the average values for 49 tropical tree species ($t_m = 0.880$) found by Sebbenn (2001).

All unilocus crossing rates were lower than the multilocus rates. This fact highlights the lack of self-incompatibility mechanisms in *D. alata*. However, as the assessments were made at an advanced age (11 years) a selection for heterozygotes may have occurred, reducing the rate of selfing and, consequently, overestimating the multilocus outcrossing rate.

The difference between the multilocus outcrossing and unilocus rates results in the outcrossing rate between endogamic or related individuals (Gusson, 2006). The rate varied among populations from 0.012 in Capinópolis to 0.004 in Jequitaiá, and, only for the latter, was not significantly different from zero. Among the families of three provenances, these rates ranged from 0.066 to 0.034 in Brasilândia de Minas; in Jequitaiá from 0.072 to 0.058 and 0.073 to 0.042 in Capinópolis. The values of t_m - t_s were significantly different from zero except for family 25 (Brasilândia de Minas). These values are considered relatively low and did not differ among the provenances.

The proportions of self-pollination, half-siblings and full siblings showed the predominance of full sibling, whose rates remained in the range of 90%. In the provenances Capinópolis and Jequitaiá the proportion of self-pollination was zero. The families that stood for the highest proportions of selfing were family 25 (Jequitaiá) (7.80%) and family 25 (Brasilândia de Minas) (6.70%), for which we obtained the lowest values of half-siblings 80.86% and 81.26% respectively. The highest values of full siblings were found in Capinópolis. This probably

occurred because the landscape is predominantly grassland and plantations of soybean, which caused the *D. alata* trees to be isolated in it.

Table 4: Estimate of parameters of reproduction system in populations of *Dipteryx alata* Vog.

Parameters	Provenances		
	Capinópolis	Jequitaiá	Brasilândia de Minas
Multilocus outcrossing rate (\hat{t}_m)	1.00 (0.000)	0.990 (0.010)	1.00 (0.000)
Unilocus outcrossings rate (\hat{t}_s)	0.988 (0.003)	0.986 (0.003)	0.995 (0.002)
Outcrossing rate among relatives ($\hat{t}_m - \hat{t}_s$)	0.012 (0.003)	0.004 (0.010)	0.005 (0.002)
Correlation of selfing (\hat{r}_s)	0.110 (0.000)	0.090 (0.02)	0.011 (0.000)
Paternity correlation (\hat{r}_p)	0.044 (0.013)	0.053 (0.018)	0.060 (0.018)
Mean number of pollen donors ($1/\hat{r}_p$)	22.72	18.86	16.66
Proportion of selfing siblings (P_{IA})	0.00%	1.00%	0.00%
Proportion of full sibs (P_{FS})	4.40%	5.25%	6.00%
Proportion of half-siblings (P_{HS})	95.60%	93.75%	94.00%

()= standard error

Conclusion:

The provenance/progeny trial of *Dipteryx alata* Vog. presents high genetic diversity in the three studied provenances.

The provenances expressed high potential to search for genotypes for genetic improvement, mainly because of the large variability found within populations.

A mixed mating system with predominance of crossing was detected in accordance to other studies.

ACKNOWLEDGEMENT

Thanks to FAPEMIG for funding the project (CAG APQ 3838.3-10/07).

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