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CELLULAR AND MOLECULAR BIOLOGY

Molecular differentiation between *Plinia cauliflora* (Mart.) Kausel and *Plinia trunciflora* (O. Berg) Kausel using nuclear SSR markers

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Abstract: Molecular markers are important tools for genetic studies, including evolution, species differentiation, and population genetics. The genus *Plinia* (Myrtaceae) consists of various fruit tree species, some of which are referred to as jaboticaba. The subtle interspecific morphological differences among some jaboticaba species make their taxonomy challenging. This study aimed to develop nuclear SSR markers to distinguish and analyze the genetics of two jaboticaba species, *Plinia cauliflora* and *Plinia trunciflora*. The developed markers – eight for *P. cauliflora* and seven for *P. trunciflora* – were cross-amplified in both species. Jointly, these markers presented high discriminatory power, private alleles at the species level, and distinguished populations of both species.

Key words: Microsatellite markers, genetic diversity, molecular markers, jaboticaba.

INTRODUCTION

The taxonomy of tribe Myrteae (Myrtaceae) is considered particularly difficult (Vasconcelos et al. 2017) due to morphological conservatism, relatively homogeneous flowers, and the rarity of unique diagnostic characters for individual clades (Lucas et al. 2019). Not all reproductive characters support the separation of Myrtaceae species, and some genera have a weak delimitation among species (Oliveira et al. 2019). Indeed, the subtle interspecific morphological differences make the taxonomy of the *Plinia* species difficult in scientific literature (dos Santos et al. 2021). This lack of consensus directly affects species selection, domestication, and reproduction studies. Integrating genetic analyses can provide more accurate information for the taxonomic classification and conservation of these genetic resources.

Shinohara et al. (2021) reported the development of a single nuclear SSR locus to differentiate *Plinia jaboticaba* 'cultivars', showing that such markers, along with plastome-based analysis (e.g., dos Santos et al. 2021, Machado et al. 2022), can effectively differentiate *Plinia* species. Aiming at generating new genomic tools for *Plinia* spp., this study reports the development of SSR genetic markers for *P. cauliflora* and *P. trunciflora* and their usefulness for species taxonomic differentiation at the molecular level.

MATERIALS AND METHODS

Whole-genome low-coverage sequencing was conducted for a single individual of each species to prospect for nuclear SSR markers. Such loci are widely distributed across the genome and

do not require deep sequencing for reliable identification, allowing for optimization of time and resources. For *Plinia cauliflora*, a total of 1.753.597.007 bp were obtained, corresponding to approximately 5× depth coverage (based on a 351 Mb reference genome; Zhao et al. 2024). For *Plinia trunciflora*, 130.267.748 bp were generated; although no reference genome is available, it may represent around 0.4× depth coverage if the genome size is similar to *P. cauliflora*. DNA was isolated from healthy leaves using the CTAB method (Doyle & Doyle 1987). Individual genomic libraries were prepared with the SQK-LSK 109 Ligation Sequencing Kit (ONT) and sequenced on a MinION Mk1B platform (ONT) using R9.4 flowcells. Vouchers of the sampled individuals were deposited in the herbarium of the UTFPR/DV (DVPR002095 for *P. cauliflora* and DVPR002097 for *P. trunciflora*). Basecalling was performed using Guppy software (ONT), and trimming and contig assembly were conducted using CLC Genomics Workbench 8.0.1 (Qiagen).

SSR loci were identified using GMata 2.3 (Wang & Wang 2016), with a minimum number of six repeats for dinucleotides (dimers) and five for trinucleotides (trimers). Primers were designed using Primer3 (Untergasser et al. 2012). SPCR 3.0 (Cao et al. 2005) was used for virtual PCR amplification and gel electrophoresis of the prospected SSR loci, using the sequenced genomes as templates. SSR loci that returned amplification products within the expected size without overlapping with nonspecific amplified products were considered potentially informative and used for wet-lab validation. The genomic origin of the loci was characterized as gene-linked nuclear, neutral nuclear, plastid, or mitochondrial through BLAST analysis of the contigs against the GenBank database. After locus characterization, sequencing data were deposited in GenBank.

Adult individuals were sampled from one natural population of each species: *Plinia trunciflora*, in the municipality of Imbituva (IMB), and *Plinia cauliflora* in the municipality of Chopinzinho (CHO), both in the state of Paraná, Southern Brazil. Individuals were also selected from plantations: one population of *P. trunciflora* (SEt) and one of *P. cauliflora* (SEc), both located in the municipality of Seara, state of Santa Catarina, Southern Brazil. In total, 39 individuals were sampled in IMB, 49 in CHO, 25 in SEt, and 52 in SEc. These samples were used for marker validation through PCR genotyping. Total DNA was isolated from healthy leaves following the CTAB protocol. DNA quantity and quality were determined using a NanoDrop 1000® spectrophotometer.

PCR reactions were performed in a Veriti® or a Biometra TProfessional thermocycler. Each reaction contained 1.0× PCR buffer, 1.5 µl $MgCl_2$ (25 mM), 1 U Taq DNA polymerase, 2.5 mM of each dNTP, 1.0 µM forward primer with a M13-tail at the 5'-end, 2.5 µM reverse primer, 2.5 µM M13-labeled fluorescent primer (6-FAM or HEX dyes), and 100 ng template DNA (Schuelke 2000). The PCR program consisted of a denaturation step at 95 °C/15 min, 10 cycles at 94 °C/1 min, 60 °C/1 min (-1 °C per cycle), and 72 °C/1 min, followed by 25 cycles at 94 °C/1 min, 50 °C/1 min, 72 °C/1 min, and a final step of 72 °C/20 min.

Alleles were resolved by capillary electrophoresis using an ABI 3500xL Genetic Analyzer (Applied Biosystems™) with POP-7™ polymer and GeneScan 600-LIZ standard. Allele sizing and genotyping were performed using GeneMapper® 4.1 (Applied Biosystems™).

The total number of alleles (*A*), effective number of alleles (*Ae*), number of private alleles, observed heterozygosity (*Ho*), expected heterozygosity (*He*), fixation index (*F*), and probability of identity (*PI*) were estimated using GenAlEx (Peakall & Smouse 2012). Genetic

structure between species was explored using the Analysis of Molecular Variance (AMOVA). A Principal Coordinates Analysis (PCoA) was performed based on the pairwise genetic distances between individuals, using GenAlEx. Finally, a Bayesian clustering approach was conducted using Structure software (Pritchard et al. 2000).

RESULTS

After sequencing, cleaning, and assembling, 3.58×10^8 base pairs were obtained for *P. cauliflora* and 3.85×10^8 for *P. trunciflora*, with *Q*-score > 20. A total of 24,100 dinucleotides and trinucleotides SSR loci were prospected for *P. cauliflora* and 9,926 for *P. trunciflora*.

Based on *in silico* validation, thirty nuclear markers (fifteen for *P. cauliflora* and fifteen for *P. trunciflora*) that successfully amplified within the expected size, and produced distinct, non-overlapping bands (without cross-amplification or non-specific products), were chosen for wet-lab validation. After bench tests, fifteen markers were selected, eight for *P. cauliflora* and seven for *P. trunciflora*. Among the markers selected *for P. cauliflora*, five were dimers and three were trimers. The seven markers developed for *P. trunciflora* are dimers. All markers were characterized as nuclear neutral or did not match any sequence in the NCBI database.

The number of alleles (*A*) and effective number of alleles (*Ae*) in *P. trunciflora* presented larger genetic variability, with up to nine alleles per locus and *Ae* reaching 4.108. *Plinia cauliflora* showed a significantly more restricted diversity pattern (maximum *A* = 4 and maximum *Ae* = 2.1). The observed heterozygosity (*Ho*) was generally higher in *P. trunciflora*, although *P. cauliflora* presented *Ho* = 1.0 in several loci (Table I). The fixation index (*F*) in *P. trunciflora* ranged from *F* = - 0.594 to *F* = 0.418 and from *F* = -0.981 to *F* = 0.496 in *P. cauliflora* (Table I). Private alleles with a frequency higher than 10% (Table I) were found in *P. trunciflora* (45 alleles) and *Plinia cauliflora* (23 alleles). The probability of identity (*PI*) of the 15 markers was $PI = 2.1\times10^{-4}$ for *P. cauliflora* and $PI = 1.6\times10^{-10}$ for *P. trunciflora*.

The AMOVA analysis indicated that 85% of genetic variation is found between species, with 15% attributed to variation within species (Figure 1a). Principal Coordinate Analysis based on the pairwise genetic distance among all samples revealed a clear separation between the species. The first two axes explained 94.34% of the total genetic variation, with two well-defined and non-overlapping clusters (Figure 1b).

The Structure analysis revealed a clear separation between *P. cauliflora* and *P. trunciflora*. Samples of *P. cauliflora* present homogeneous genetic profiles, while *P. trunciflora* revealed distinct clusters for the natural population and the plantation (Figure 1c).

DISCUSSION

The name 'jaboticabeira' is widely used to refer to several species belonging to the genera *Plinia* or *Myrciaria* (Espíndola 2018). In Brazil, nine distinct species have been recorded. The taxonomic delimitation of these species has been revised, since their morphological similarity often makes accurate identification difficult (Miranda et al. 2024). *Plinia trunciflora* is characterized by elliptical, oblong, or lanceolate leaves, tetramerous flowers with ovate, oblong, or obovate petals, and globose fruits with elongated peduncles (Espíndola 2018). Similarly, *P. cauliflora* is recognized by its smooth trunk, elliptical to ovate leaves, and globose fruits (Espíndola 2018).

The SSR markers developed in this study distinguished *P. cauliflora* and *P. trunciflora* as two genetically distinct species. The analysis of

Table I. Characteristics of SSR markers developed for *P. cauliflora* (CAU set) and *P. trunciflora* (TRU set), including primer sequences, expected product sizes according to the sequenced loci, and estimations of total number of alleles (*A*), effective number of alleles (*Ae*), observed heterozygosity (*Ho*), expected heterozygosity (*He*), fixation index (*F*), number of private alleles (*pA*) with frequency lower than 10%, and number of private alleles with frequency higher than 10%.

Locus	Primer sequence (5' - 3')	Motif	Expected allele size (bp)	*A*[$]	*Ae*	*Ho*	*He*	*F*	*pA* <10%	*pA* >10%
CAU2	F: TCCTTGGTATCTGGGAGCAC R: ACTACACGCGTTGAGCCTTT	$(TTA)_6$	283	Pc = 2 Pt = 2	Pc = 1.01 Pt = 1.77	Pc = 0.01 Pt = 0.64	Pc = 0.01 Pt = 0.43	Pc = -0.005 Pt = -0.471	Pc = 1 Pt = 2	Pc = 1 Pt = --
CAU3	F: TTCTAACCTAAGGCGCTTGC R: TGGCAAAAGTCAACAGACCA	$(AAG)_6$	224	Pc = 3 Pt = 5	Pc = 1.02 Pt = 2.79	Pc = 0.01 Pt = 0.97	Pc = 0.02 Pt = 0.64	Pc = 0.496 Pt = -0.509	Pc = 1 Pt = 3	Pc = 2 Pt = 2
CAU6	F: GCAACTTGTCCCTGTGATGA R: TTTCATCCATGCACTCCAAA	$(AT)_7$	302	Pc = 3 Pt = 5	Pc = 2.02 Pt = 3.83	Pc = 1.00 Pt = 0.97	Pc = 0.50 Pt = 0.74	Pc = -0.981 Pt = -0.311	Pc = 2 Pt = 4	Pc = 1 Pt = 1
CAU7	F: GGAAGGAACCACAGGATCAA R: AGGCTTGGTGTTTCATGAGG	$(AAT)_6$	276	Pc = 3 Pt = 9	Pc = 2.02 Pt = 4.11	Pc = 1.00 Pt = 1.00	Pc = 0.50 Pt = 0.76	Pc = -0.981 Pt = -0.322	Pc = 2 Pt = 4	Pc = 1 Pt = 5
CAU8	F: CCGAGAATCCCATCTTCTCA R: GCCATCTCCGTTTTATCCAA	$(AG)_6$	355	Pc = 1 Pt = 5	Pc = 1.00 Pt = 2.68	Pc = 0.00 Pt = 1.00	Pc = 0.00 Pt = 0.63	Pc = N/A Pt = -0.594	Pc = 1 Pt = 3	Pc = -- Pt = 2
CAU11	F: AATGGATCGCTGTCTCCATC R: CGGTCCCACATCATTCTCTT	$(CT)_{19}$	347	Pc = 4 Pt = 7	Pc = 2.10 Pt = 3.99	Pc = 1.00 Pt = 0.98	Pc = 0.52 Pt = 0.75	Pc = -0.909 Pt = -0.313	Pc = 2 Pt = 4	Pc = 2 Pt = 3
CAU12	F: ACCATTCCATCCTCTCCAAG R: GAATGGGCGGATCTAGGTTT	$(TC)_{19}$	217	Pc = 3 Pt = 3	Pc = 1.17 Pt = 1.85	Pc = 0.16 Pt = 0.67	Pc = 0.15 Pt = 0.46	Pc = -0.081 Pt = -0.458	Pc = 1 Pt = 2	Pc = 2 Pt = 1
CAU14	F: CTTTGCGTCTGACCTTGAAA R: TGTCCGGCTAGCTATTTTGG	$(TC)_{15}$	362	Pc = 3 Pt = 4	Pc = 2.02 Pt = 2.19	Pc = 1.00 Pt = 0.33	Pc = 0.50 Pt = 0.54	Pc = -0.981 Pt = 0.397	Pc = 2 Pt = 3	Pc = 1 Pt = 1
TRU1	F: CCATTGTTGTTTAGCCTGGAA R: ATCTCAGCTCAAGCCTGTGG	$(TG)_8$	254	Pc = 1 Pt = 5	Pc = 1.00 Pt = 2.01	Pc = 0.00 Pt = 0.34	Pc = 0.00 Pt = 0.50	Pc = N/A Pt = 0.315	Pc = 1 Pt = 3	Pc = -- Pt = 2
TRU2	F: CGAAACGTAAAACGCTCGAA R: ATTGCAACAGGACCTCCAAA	$(TC)_{13}$	258	Pc = 3 Pt = 4	Pc = 2.02 Pt = 1.55	Pc = 1.00 Pt = 0.34	Pc = 0.50 Pt = 0.36	Pc = -0981 Pt = 0.036	Pc = 2 Pt = 2	Pc = 1 Pt = 2
TRU5	F: TGTTACATGCCGTGGGACTA R: TTTGGGGTAATCGATGAAGG	$(CT)_{16}$	344	Pc = 2 Pt = 4	Pc = 1.01 Pt = 1.44	Pc = 0.01 Pt = 0.33	Pc = 0.01 Pt = 0.31	Pc = -0.005 Pt = -0.077	Pc = 1 Pt = 2	Pc = 1 Pt = 2
TRU7	F: TATGCAAGTCTGCCGTTGAG R: CTTTCTGGCGAGTTGAGAGG	$(TC)_{36}$	305	Pc = 3 Pt = 3	Pc = 2.02 Pt = 2.99	Pc = 1.00 Pt = 0.63	Pc = 0.50 Pt = 0.66	Pc = -0.981 Pt = 0.061	Pc = 2 Pt = 3	Pc = 1 Pt = --
TRU9	F: CCAAGGGTGCAATGTTGTAA R: GGTTCCACCAGAACAAAGGA	$(CT)_{10}$	400	Pc = 3 Pt = 6	Pc = 2.02 Pt = 2.23	Pc = 1.00 Pt = 0.37	Pc = 0.50 Pt = 0.55	Pc = -0.981 Pt = 0.320	Pc = 2 Pt = 3	Pc = 1 Pt = 3
TRU14	F: TGTACGTTGAGGATTGACTCG R: CTGGTCGTTCACATCATTGG	$(CT)_7$	261	Pc = 4 Pt = 3	Pc = 2.04 Pt = 2.16	Pc = 1.00 Pt = 0.31	Pc = 0.51 Pt = 0.54	Pc = -0.962 Pt = 0.418	Pc = 2 Pt = 3	Pc = 2 Pt = --
TRU15	F: CCCATGAGGGGAGTGATCTA R: GATCAACCTGACCCCAAGAA	$(AG)_8$	328	Pc = 1 Pt = 7	Pc = 1.00 Pt = 4.03	Pc = 0.00 Pt = 1.00	Pc = 0.00 Pt = 0.75	Pc = N/A Pt = -0.330	Pc = 1 Pt = 4	Pc = -- Pt = 3

[$]: Pc = *Plinia cauliflora*; Pt = *Plinia trunciflora*; N/A = not applied.

molecular variance based on genotypic structure revealed 85% of the variation between species, and the principal coordinate analysis delimited two genetic clusters without any overlap, a pattern also returned by the Bayesian structure analysis. The Bayesian clustering analysis also showed high genetic homogeneity between the natural population and the commercial orchard of *P. cauliflora* (which seems to be formed mostly by clones and is being further investigated). These findings highlight the evolutionary divergence between *P. cauliflora*

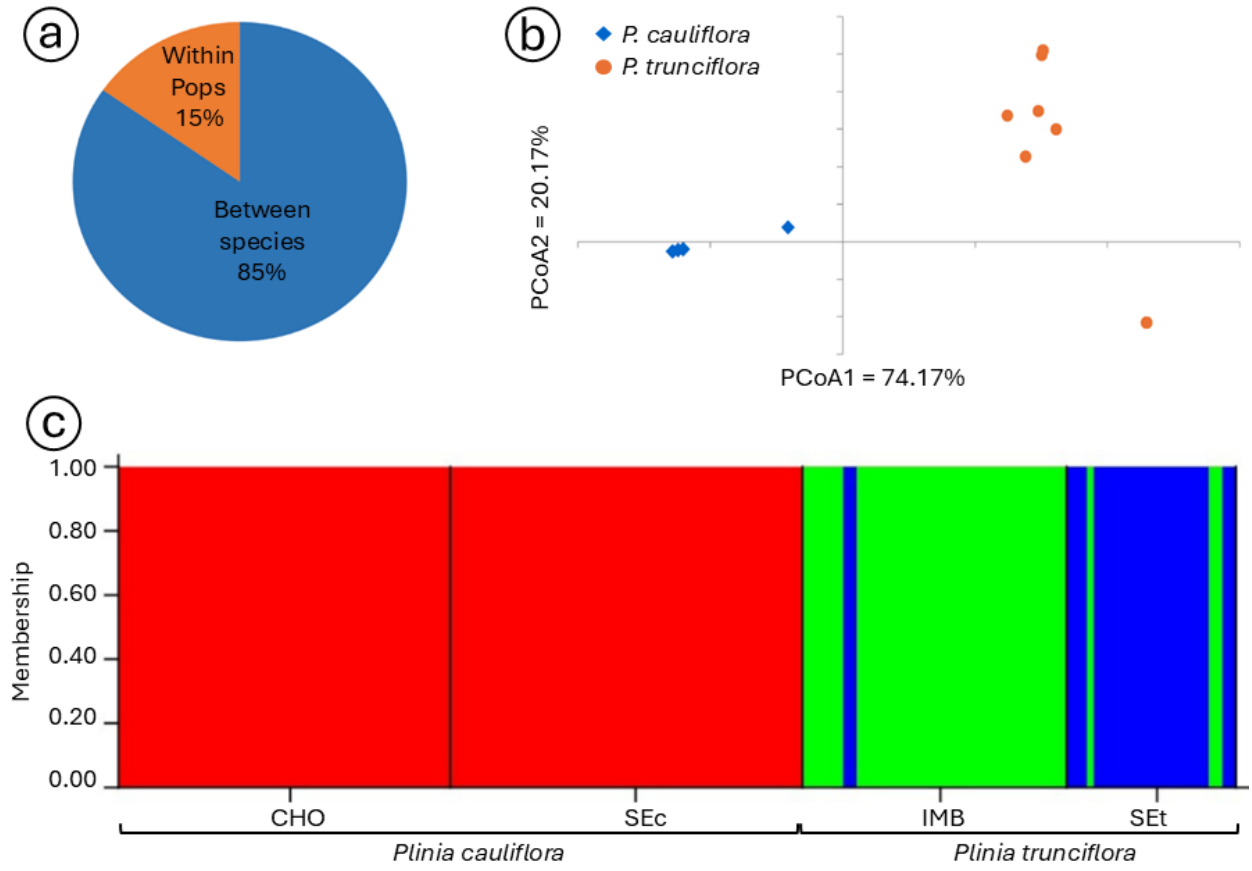

Figure 1. Genetic structure between *Plinia cauliflora* and *Plinia trunciflora*. a) AMOVA analysis of the four populations of both species. b) Principal coordinates analysis based on pairwise genetic distance between individuals. c) Bayesian structure analysis (STRUCTURE) for *K* = 3. CHO: Chopinzinho (natural population of *P. cauliflora*); SEc: plantation of *P. cauliflora*; IMB: Imbituva (natural population of *P. trunciflora*); SEt: plantation of *P. trunciflora*.

and *P. trunciflora*, reinforcing their taxonomic distinction and providing insights relevant for conservation and breeding programs. On the other hand, *P. trunciflora* exhibited significant genetic divergence between the sampled populations. The markers' discriminatory power is also supported by the presence of private alleles in both species, which may be further exploited as markers for species differentiation. Private SSR alleles reported in *Psidium* (Myrtaceae) were useful in distinguishing closely related species and identifying unique variants with adaptive potential (Tuler et al. 2015). SSR markers also resulted in a clear genetic structuring between wild and cultivated genotypes for *Psidium guajava* (Kumar et al. 2020).

Furthermore, the data obtained may enhance our understanding of the genetic diversity and structure of *P. trunciflora* and *P. cauliflora* populations. The markers' classification as nuclear and neutral supports their applicability in studies of genetic diversity, population structure, and conservation (Serrote et al. 2023), while the *PI* estimations confirm their informative power. *Plinia trunciflora* showed higher genetic diversity compared to *P. cauliflora*, concerning *Ho*, *A*, and *Ae*. On the other hand, populations from both species presented negative fixation index estimations, suggesting a

complex genetic structure influenced by random crossings and an excess of heterozygotes. These negative estimations may reflect a recent history of population restriction, such as geographic isolation or the effects of domestication, vegetative reproduction, and antropogenic use.

CONCLUSIONS

In addition to clarifying the taxonomic differentiation between these two *Plinia* species, the newly developed SSR markers represent valuable molecular tools for the conservation, improvement, and sustainable use of *P. cauliflora* and *P. trunciflora*. These markers can be applied in breeding programs to select superior genotypes, identify potential hybrids, and protect newly developed cultivars.

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Data availability

The sequences of the SSR primers are deposited in the NCBI/GenBank database. Further data may be obtained from the Authors.