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Biotechnology in *Plinia* spp. needs and perspectives for a neglected group of fruit species

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ABSTRACT

Plinia species comprise a group of underrated fruit trees native to the South and Central American neotropics. Their fruits have high potential as a nutraceutical food and to the medicinal industry. However, among the 80 accepted species, less than a dozen are cultivated. In this review, the state-of-the-art of the genetic diversity and the techniques of vegetative propagation of *Plinia* spp. was updated. Therewith, it is intended to encourage further studies for genetically disentangle the taxonomic classification the species, and the development of propagation protocols towards the establishment of commercial plantations. Establishing commercial orchards of *Plinia* species may open new markets for this fruit crop, but the absence of breeding programs and superior quality seedlings hinder such endeavors. The main outcomes of this study are the need of using molecular approaches for solving the taxonomic uncertainties among *Plinia* species and micropropagation protocols to overcome the difficulties concerning to the vegetative propagation of this species.

Keywords: biotechnology, jaboticabeira, micropropagation, molecular taxonomy, morphological diversity, vegetative propagation

Biotecnología en *Plinia* spp. necesidades y perspectivas para un grupo desatendido de especies frutales

RESUMEN

Las especies de *Plinia* comprenden un grupo subestimado de árboles frutales nativos de los neotrópicos de América del Sur y Central. Sus frutos tienen un alto potencial como alimento nutracéutico y para la industria medicinal. Sin embargo, entre las 80 especies aceptadas, se cultivan menos de una docena. En esta revisión, se actualizó el estado del arte de la diversidad genética y las técnicas de propagación vegetativa de *Plinia* spp. Con ello, se propondrá impulsar nuevos estudios para dilucidar genéticamente la clasificación taxonómica de la especie y el desarrollo de protocolos de propagación hacia el establecimiento de plantaciones comerciales. El establecimiento de plantaciones comerciales de especies de *Plinia* puede abrir nuevos mercados para este cultivo de frutas, pero la ausencia de programas de mejoramiento genético y plántulas de calidad superior obstaculizan tales esfuerzos. Los principales resultados de este estudio son la necesidad de utilizar enfoques moleculares para resolver las incertidumbres taxonómicas entre las especies de *Plinia* y los protocolos de micropropagación para superar las dificultades relacionadas con la propagación vegetativa de esta especie.

Palabras clave: biotecnología, diversidad morfológica, jaboticabeira, micropropagación, propagación vegetativa, taxonomía molecular

INTRODUCTION

Jaboticabeira is the popular name of different species of the genus *Plinia* L. (Myrtaceae), native to the South and Central American neotropics (Figure 1 A). The main characteristic of these trees (Figure 1 B) is the development of flowers and fruits (popularly known as jaboticaba) over the wood trunk and main stems (Figure 1 C-D), a feature known as cauliflory. Reproductive buds of *Plinia* initiate from vascular cambium cells through cell division followed by an increase in the size of the meristematic region from the vascular cambium toward both the bark and the xylem, keeping the connection with vessel elements (Oliveira *et al*., 2019).

Fruits are produced once or twice a year, eventually up to three times, depending on climatic conditions and the management adopted. In *Plinia jaboticaba*, it seems that inflorescence sprouting is stimulated by low temperatures and water deficit (Oliveira *et al*., 2019). The fruits have economic potential both for fresh consumption and in the food and pharmaceutical industries. They present a wide variety of classic nutrients and components capable of providing positive physiological effects on health (Teixeira *et al*., 2008; Rufino *et al*., 2011). They also have recognized antioxidant properties, protecting from damages caused by free radicals, preventing or postponing the onset of cardiovascular, chronic, and neurodegenerative diseases (Pitz *et al*., 2017).

Figure 1. (A) Distribution of *Plinia* species in neotropical South and Central America according to the Plants of the World platform (www.plantsoftheworldonline.org). CU: Cuba, HA: Haiti, SD: San Domingo, BZ: Belize, GU: Guatemala, HO: Honduras, CR: Costa Rica, PN: Panamá, CO: Colombia, VE: Venezuela, GU: Guyana, SU: Suriname, EQ: Equador, PE: Peru, BO: Bolivia, BR: Brazil, PY: Paraguay, AR: Argentina, UR: Uruguay. (B) Adult tree of *Plinia peruviana*. growing in an urban backyard. (C) Flowers growing along the tree stem. (D) Rip fruits along the tree stem.

In this context, this review aims at updating the state-of-the-art of the taxonomic and genetic diversity and the techniques of vegetative propagation of *Plinia* spp. Therewith, it is intended to encourage the development of further studies for genetically disentangle the taxonomic classification of the *Plinia* species, and the development of propagation protocols towards the establishment of commercial plantations, attempting the market valuation of the fruit.

Expanding genetic and genomic analyses are needed to disentangle the subtle inter-species morphological differences

The jabuticabeiras were firstly taxonomically described into genus *Myrtus* Tourn ex. L. and *Guapurium* Juss. and were relocated within genus *Myrciaria* O. Berg (Berg, 1857). As some floral traits diverged from other species of genus *Myrciaria*, species of jabuticabeira were transferred to genus *Plinia* (Kausel, 1956; Sobral, 1985; Mattos, 1998). Currently, 80 species of *Plinia* are accepted (Govaerts *et al*., 2008).

Given the morphological variation observed in characteristics of fruits (Table 1, Table 2 and Table 3), the taxonomy of *Plinia* species is fairly a puzzle in the scientific literature. A miscellaneous of different species is suggested by diverging authors, making advances in selection, domestication, and breeding difficult.

Besides recognizing the morphological multiplicity, understanding the genetic divergence among species can be useful for the comprehension and conservation of the available genetic resources. Moreover, the morphological differences among some *Plinia* species are rather modest, making the species delimitation a great challenge for breeders and farmers.

Despite these needs, only a few studies using molecular markers were published, reporting the comparative analysis among different species of *Plinia*. Pereira *et al*. (2005) used 45 polymorphic RAPD markers in a study including *P. jaboticaba, P. cauliflora, P. coronata,* and *P. phitrantha*, while Vilela *et al*. (2012) used 37 polymorphic RAPD markers to study the relationship among *P. cauliflora, P. jaboticaba, P. coronata,* and *P. peruviana.* In both studies, clustering analyses were unsuited for defining the taxonomic groups, since the formed clusters comprised assortments of plants from different species and did not correspond to the taxonomic classifications based on morphological traits. Moreover, RAPD markers are not confident for such an analysis, due to several technical weaknesses.

The advances of the sequencing platforms have enabled researchers to generate comprehensive genomic data for several plant species, including also minor-crop species. Sequences of the complete chloroplast genome (plastome) of *P. cauliflora, P. aureana,* and *P. trunciflora* are available in the GenBank database. To test the usefulness of these molecular data for understanding the taxonomic relationship among *Plinia* species, the plastome sequences of *P. cauliflora* (KX527622; Machado *et al*., unpublished), *P. aureana* (KY392759; Machado *et al*., unpublished), *P. trunciflora* (KU318111; Eguiluz *et al*., 2017), *Acca sellowiana* (KX289887; Machado *et al*., 2017), *Campomanesia xanthocarpa* (KY392760; Machado *et al*., 2020), and *Allosyncarpia ternata* (KC180806; Bayly *et al*., 2013) were downloaded and a phylogenomic analysis was performed. This analysis (Figure 2) enabled more accurate analysis of the correlation among these *Plinia* species. Although the length, genetic composition, and structure of the plastomes are conserved among these species, the phylogenomic analysis based on the whole plastomes sequences resolved these three species with high support (Figure 2).

Thus, sequencing the plastomes of more *Plinia* species seems to be a meaningful strategy for resolving the remaining taxonomic uncertainties in this group, aiding the planning of conservation and breeding programs for *Plinia* species.

Germplasm conservation and genetic improvement also need molecular genetic studies

Information about the genetic diversity of natural populations is also needed when aiming at the establishment of germplasm banks and genetic improvement of the species (Melo *et al*., 2015). Cruz *et al*. (2016) evaluated the genetic diversity of *Plinia* spp. in Northeastern

Table 1. Morphological characteristics of *Plinia cauliflora*, *P. jaboticaba* and *P. aureana* according to Lorenzi (2000), Lorenzi *et al*. (2006), and Lorenzi (2011).

Species	Characteristics			
	Tree	Leaves	Flowers	Fruits
Plinia cauliflora	- Height: 3-9 m - Dense cup - Tortuous trunk, with smooth, light brown, and spotted bark.	- Length: 3 - 7 cm - Glabrous - Lanceolate to oblong-lanceolate blade, with acuminate apex and acute or obtuse base.	- White color - Very short pedicels of about 1 mm, uniflorous, with ciliated bracts - Glabrous floral button - Chalice with cylindrical lobes - Petals largely oblong.	- Diameter: 2.2 - 2.8 cm - Globous, smooth and shiny berry - Dark purple color - Pulp is generally sweet.
Plinia jaboticaba	- Height: 4-9 m - Dense cup - Knotty and tortuous trunk, with smooth and thin bark of uniform brownish-brown color or with lighter spots.	- Length: 2.4 - 4.3 cm, - Lanceolate blade, with acute apex and obtuse base, - Glabrous (except for the central rib on the underside).	- White color, - inflorescence in a fascicle, with medium pedicels, and hairy bracts imbricated and irregularly arranged, - Chalice with 4 ovate, ciliated, and unequal lobes.	- Diameter: 2.2 - 2.8 cm, - Globous berry and thin skin, - Dark purple color, - Sweet pulp.
Plinia aureana	- Height: 2-4 m - Dense pyramidal cup, - Tortuous and fluted trunk, with reddish-brown and spotted bark.	- Length: 5.5 - 11.0 cm, - Oblong or lanceolate blade, with a gradually accentuated apex and rounded base, - Glabrous on the upper face and sparse hair on the lower.	- White color, - Pedicels of 1 - 3 mm, - Obovate floral button with sparse hair, - Hairy bracts of just over 1 mm, - Glabrous petals about 2 mm long.	- Diameter: 1.0 - 2.5 cm, - Subglobosa-oblique berry, side and glabrous, - Light green color, - Very sweet pulp.

Brazil. Thirty-five genotypes were characterized using ISSR (Inter Simple Sequence Repeats) markers. With a polymorphism of 99.65%, five groups were identified based on the genetic divergence among genotypes. Moreover, no correlation between geographical and genetic distances among genotypes was observed. This study revealed the existence of moderate genetic variability of the studied genotypes, an important insight regarding plant collection for breeding programs in the region.

The organization and distribution of population genetic variability of six populations of *P. peruviana* based on microsatellite markers were reported by Salla (2019). Ten microsatellite loci revealed significant genetic diversity for the six populations, with a high number of alleles and heterozygosis. The analyses of the molecular diversity partition revealed 17.6% of differentiation among populations, 2.6% within populations, and 72.2% within individuals. These results suggest that for conservation proposes, seed

Table 2. Morphological characteristics of *Plinia coronata*, *P. grandifolia* and *P. oblongata* according to Lorenzi (2000), Lorenzi *et al*. (2006), and Lorenzi (2011).

Species	Characteristics			
	Tree	Leaves	Flowers	Fruits
Plinia coronata	- Height: 3-12 m, - Elongated cup, - Ribbed trunk, light brown and stained.	- Length: 4 - 6 cm, - Lanceolate blade, with acuminate apex and rounded base, - Glabrous, and pubescence only on the main vein (both sides).	- White color, - Clusters of 1 - 6, with pedicels of about 1 - 2 mm, surrounded by 4 rows of nested and ciliated bracts, - Oval-oblong and cylindrical petals.	- Diameter: 2.5 - 3.5 cm, - Globous berry. - Dark purple color, with whitish disc outline, apex. - Acidic pulp.
Plinia grandifolia	- Height: 4 - 8 m, - Dense cup, - Trunk somewhat tortuous and ribbed, with smooth brownish-brown bark with lighter spots.	- Length: 7 - 11 cm, - Oblong and oblong-lanceolate blade, with acuminated apex and obtuse base, - Glabra.	- White color, - Inflorescences with hairy pedicels, and equally hairy deciduous bracts, - Chalice with cylindrical sepals, - Petals largely obovate.	- Diameter: 1.5 - 2.5 cm, - Globous and smooth berry, - Dark purple color, - Acidic or sweet pulp.
Plinia oblongata	- Height: 4 - 6 m,	- Length: 2.0 – 4.5 cm, - Glabrous, and pubescence only on the main vein (both sides), - Ciliary margin.	- White color, - Pedicels very short and hairy with about 2mm and the base is surrounded by bracts.	- Diameter: 2.5 - 3.0 cm, - Slightly ovate-elliptical to elliptical, and smooth, - Dark purple color, - Very acidic pulp.

collections should maximize the number of seeds per matrix plant, lessening the number of individuals per population (Salla, 2019).

This scarcity of genetic studies and the small geographical amplitude of the two existing studies with *Plinia* spp. natural populations hinders planning reliable programs of *in situ* or *ex situ* species conservation, seed collection, genotype selection, and genetic improvement. So, efforts towards characterizing the genetic diversity and structure of *Plinia* spp. natural populations using molecular markers and in a wider geographical perspective is needed.

Moderate to low rooting rates is the main limitation for traditional vegetative propagation of *Plinia* species

A review on the propagation of *Plinia* spp. by Silva *et al*. (2018) highlighted that the main form of seedling production is still carried out mainly by seeds, due to the greater ease and speed in the production of new plants. However, despite good germination rates, seed recalcitrance (Danner *et al*., 2011; Hössel *et al*., 2013) hampers the establishment of orchards through sexual propagation and studies about the conditions of seed germination of *Plinia* species (Andrade and Martins, 2003; Wagner *et al*., 2006; Alexandre

Table 3. Morphological characteristics of *Plinia peruviana*, *P. phitrantha* and *P. spiritosantensis* according to Lorenzi (2000), Lorenzi *et al*. (2006), and Lorenzi (2011).

Species	Characteristics			
	Tree	Leaves	Flowers	Fruits
Plinia peruviana	- Height: 4 - 14 m, - Dense and globose cup, - Straight and knotty trunk, with smooth brownish-brown bark with lighter spots.	- Length: 2 - 7 cm, - Lanceolate to the ovate-lanceolate blade, with long-acuminate apex and obtuse or corded base.	- White color, - Inflorescence (4 to 8 flowers) in racemes, with an almost zero primary axis and several pubescent pedicels of 10 - 15 mm, - Globose floral bud of about 0.5 cm in diameter.	- Diameter: 1.8 - 2.5 cm, - Globous berry, - Dark purple color, - Sweet pulp.
Plinia phitrantha	- Height: 4 - 7 m, - Ribbed trunk, with thin brownish-yellow bark with lighter spots,	- Length: 4.0 - 14.0 cm, - Oblong to oblong-lanceolate blade, with acute apex and underlay base, - Almost glabrous on the upper side and pubescent on the lower side.	- White color, - Scaly and rounded scaly bracts at the base of the pedicels, - Chalice with 4 glabrous sepals.	- Diameter: 1.5 - 2.5 cm, - Subglobous and side, - Red to purple color, - Sweet pulp.
Plinia spiritosantensis	- Height: 3 - 6 m, - Dense cup, with smooth, brownish skin with grayish spots.	- Length: 3.2 - 9.5 cm, - Ovate-oblong or lanceolate blade, with acute or slightly acuminated apex, and corded base, - Glabrous on the upper face (except on the central rib that is hairy), and sparse-hairy on the lower.	- White color, - Hairy pedicels of 1 - 1.2 mm, - Goblets with obovate and concave, ciliated sepals, about 2 mm long.	- Diameter: 2.0 - 3.0 cm, - Globous berry, - Purplish color.

et al., 2006; Rossa *et al*., 2010; Sartor *et al*., 2010; Dias *et al*., 2011; Wagner *et al*., 2011) are puzzling and inconclusive.

The development of methods for the asexual propagation of *Plinia* spp. is of great importance for obtaining seedlings. In addition to reducing the juvenile phase, vegetative propagation has some advantages such as maintenance of the genetic characteristics of the mother plant, greater productivity, and fruits of better quality (Danner *et al*., 2006; Hartmann *et al*., 2011). However, there is no established fully efficient methods of vegetative propagation of *Plinia* spp. that ensure the formation of commercial orchards in a short period.

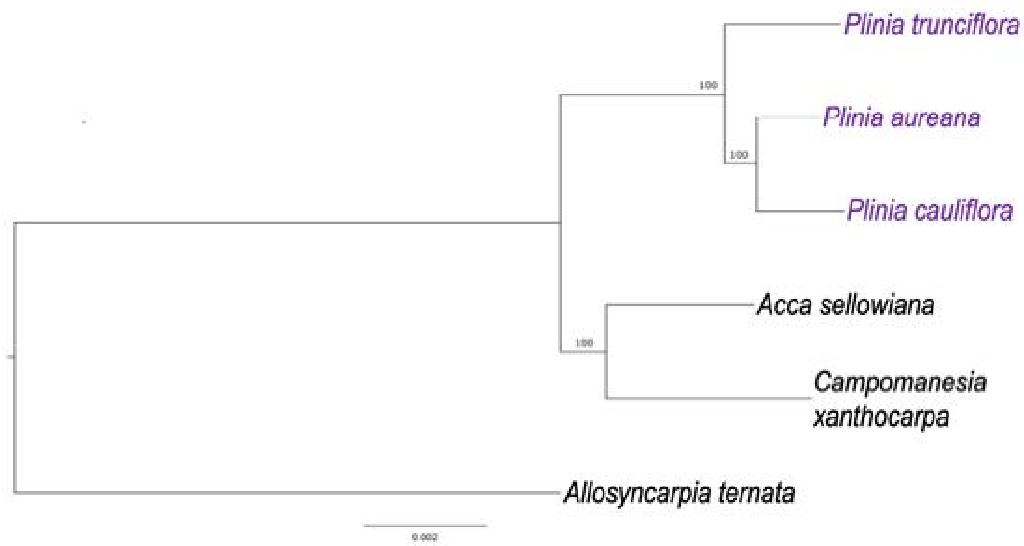

Figure 2. Phylogenomic analysis based on the whole plastome sequences of *Plinia cauliflora, P. aureana, P. trunciflora, Acca sellowiana, Campomanesia xanthocarpa,* and *Allosyncarpia ternata*. The phylogenomic tree was obtained using the maximum likelihood algorithm, the GTR+G evolution model, and 1000 bootstrap replications for branch support, as implemented in the software RAxML, CIPRES Science Gateway V. 3.1 platform. *Allosyncarpia ternata* (Myrtaceae, Eucalypteae) was employed as an outgroup. All other species belong to the family Myrtaceae, tribe Myrteae.

In general, *Plinia* species are recalcitrant for the formation of adventitious roots, and layering seems to be a relatively effective method for vegetative propagation of the species. This method, mediated by indole-butyric acid (IBA) treatment provides the gathering of numerous rooting co-factors (Danner *et al*., 2006; Sasso *et al*., 2010; Cassol *et al*., 2015). However, for the establishment of a conclusive protocol, new studies must be carried out, considering the percentage of harvesting of the transplanted seedlings, the minimum period for the disconnection of the mother plant layering, the quality of the roots formed, the time between the planting of seedlings in the field, and the beginning of fruit production.

The few studies using cutting as a propagation method in *Plinia* species (Pereira *et al*., 2005; Fachinello *et al*., 2005; Sartor *et al*., 2010; Silva *et al*., 2019) revealed rooting rates lower than 50%. For commercial seedling production, the percentage of cuttings rooting obtained should be higher than 70% (Hartmann *et al*., 2011). The values reported for *Plinia* spp. are quite variable and usually lower than this threshold. The low rooting of the vegetative propagules seems to be correlated with the age of the tissue, the type and time of collection of the cuttings, the presence or absence of growth regulators, and cuttings cultivation conditions. Therefore, several adjustments are needed to increase the rooting percentage in *Plinia* species propagated through the cutting technique.

Grafting has supported somewhat more promissory results as a vegetative propagation strategy for *Plinia* species. Setting values reaching up to 90% were reported (Manica, 2000; Sasso *et al*., 2010, Franco *et al*., 2010; Malagi *et al*., 2012; Cassol *et al*., 2017), but these results revealed to be dependent on the cultivars used and the season. Despite the optimistic results obtained, long-term field monitoring of plants produced from grafting is necessary so that compatibility is verified. Besides, it is still necessary to verify the evolution of growth in the field, and the time elapsed from grafting to the beginning of the fruiting of the grafted seedling.

Protocols of *in vitro* propagation are promising strategies for *Plinia* spp.

In vitro micropropagation is the most practical application of tissue culture and the one with

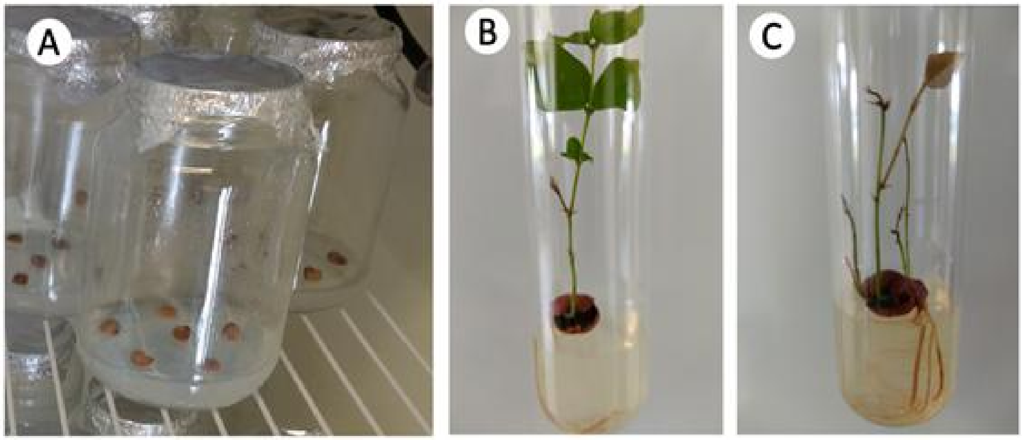

Figure 3. *In vitro* germination of *Plinia* spp. (A) *In vitro* axenic germination of seeds. (B) Germination of a single plantlet from the seed. (C) Polyembryony with four plantlets germinated from a single seed.

the greatest impact toward allowing conditions to obtain plants that are difficult to propagate and have long life cycles. This approach allows obtaining plants in an aseptic and controlled environment, faster than compared to conventional breeding. *In vitro* germination (Figure 3) can be the first step to obtain aseptic plants, which can be used as a source of propagules for micropropagation. *In vitro* germination of *Plinia* species also enables easy follow of the occurrence of polyembryony, since the number of embryos can reach up to five per seed (Figure 3C).

The *in vitro* germination of *P. jaboticaba* has been performed in MS (Murashige and Skoog, 1962) culture medium (Picolotto *et al*., 2007; Santos *et al*., 2019) and agar:water medium (5-6%, w/v). However, fungal and bacterial contaminations are the most worrisome issues. Treatments of the seeds with sodium hypochlorite (Picolotto *et al*., 2007), and soaking for 24 hours in sterile water and antibiotics (Santos *et al.,* 2019) have been the commonly used methods for seeds disinfection. Besides, the germination is also influenced by the temperature of culture, but not by the photoperiod (Picolotto *et al*., 2007), with the best germination rates at 25 ºC.

Callogenesis was obtained in *P. cauliflora* leaf explants using MS medium with different combinations of plant growth regulators: 2,4-dichlorophenoxyacetic acid (2,4-D) at 0.0, 1.0, 2.0, 4.0 mg l^{-1} + 6-benzylaminopurine (BAP) at 0.0, 0.1, 0.2 mg l^{-1} and naphthaleneacetic acid (NAA) at 0.0, 1.0, 2.0, 4.0 mg l^{-1} + BAP (0.0, 1.0, 2.0 mg l^{-1}. All treatments presented callus formation, also in absence of plant growth regulators, not differing statistically (Cardoso, 2016).

Somatic embryos at the cotyledonary stage were obtained from seed explants of *P. peruviana* by Oliveira (2018). Pro-embryogenic masses were induced in 82.5% of explants using the two cotyledons detached and cultivated in the MS medium with 300 µM of 2,4-D and 1 g l^{-1} of activated charcoal. During phase I of maturation, the most suitable medium for the conversion of somatic embryos at the torpedo stage was MS with 30 g l^{-1} of polyethyleneglycol 4000 (77.5% of the formation of embryos in the torpedo stage). There was no conversion of somatic embryos into seedlings and the formation of embryos was possible up to the cotyledonary stage (3.05%), forming abnormal embryos. Anatomical studies showed the development of asynchronous somatic embryos.

Silveira *et al*. (2020) established a somatic embryogenesis protocol for *P. peruviana* using mature seeds (two separate cotyledons) as explant, inoculated in MS medium with the addition of 1000 mg l^{-1} of glutamine, and 10 µM of 2,4-D. Larger embryos and in more advanced stages of development were obtained in a medium containing 60 g l^{-1} of polyethyleneglycol 6000. There was no conversion of somatic embryos into seedlings and anatomical sections of the embryos revealed deleterious effects of the prolonged period of exposure to 2,4-D.

Although failing to convert somatic embryos into seedlings, the studies of Oliveira (2018) and Silveira *et al*. (2020) were pioneers in the development of a somatic embryogenesis protocol for *Plinia* spp.. Thus, further studies are needed to determine the optimum exposure period to 2,4-D for the formation of somatic embryos with normal morphology, which drives conversion to seedlings.

How may biotechnology help to boost jaboticaba into the market?

The fruits of *Plinia* species have a high market value, good organoleptic characteristics, high nutritive content, and beneficial properties to health. Thus, there is a forecast of growth in demand for fresh consumption and use by industries. As the cultivation of *Plinia* spp. is practically restricted to domestic orchards and the establishment of commercial plantations demands a large amount of vigorous and uniform selected seedlings, it is necessary to develop protocols of vegetative propagation. Micropropagation seems to be the most promising technique providing seedlings on a large scale with high phytosanitary quality, regardless of the time of year.

Plastome based phylogenomic studies may be an important strategy towards understanding the taxonomic relationships among *Plinia* species, as well as to verify the validity of all proposed species. Also, genetic studies using molecular markers should be performed to characterize the genetic diversity of natural populations towards germplasm conservation and genetic improvement of the species. This biotechnological tool can also be used to evaluate the somaclonal variation of micropropagated seedlings since in clonal propagation the main purpose is the maintenance of the genetic characteristics of selected plants. Besides, to circumvent situations in which the multiplication from natural seeds is problematic, the encapsulation of vegetative structures into sodium alginate droplets and protocols for cryopreservation of embryos and cell cultures are also needed for the species.

CONCLUSIONS

Aiming at seeking the market valuation of the fruits of *Plinia* spp., studies involving molecular approaches are necessary to resolve the taxonomic uncertainties between species. In addition, the establishment of micropropagation protocols for jaboticabeira is needed to overcome the difficulties related to the vegetative propagation of these species.

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Conflict of interest

The authors declare that there is no conflict of interest regarding the publication of this article.

Authors contribution

Conceptualization, Investigation, and Writing - original draft DDS, LOO, DCB; Resources DDS; Writing-review and editing VMS; Methodology and Formal analysis DDS, LOM; Supervision VMS.

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