

Original Article

xButyagrus nabonnandii (Prosch.) Vorster (Arecaceae): a sterile and rare palm with variable morphology?

xButyagrus nabonnandii (Arecaceae): uma palmeira rara e estéril com morfologia variável?

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Abstract

xButyagrus nabonnandii (Prosch.) Vorster is known as mule palm due to sterility, but recently, its pollen has been successfully used in backcrosses. It was first described as an artificial cross between *Syagrus romanzoffiana* (Cham.) Glassman and *Butia odorata* (Barb.Rodr.) Noblick in 1890. It has been considered rare in nature, and its morphology has been little studied. Thus, we aimed to verify if *xB. nabonnandii* is sterile by studying its morphology and seed germination from different natural populations. The hybrid was sampled in four municipalities and is new to three of these. In one of the visited cities, 20 specimens were counted. The vegetative morphology showed less variation than the reproductive. However, part of the vegetative characters differed from previous descriptions relying solely on cultivated specimens. Contrary to previous reports, our data indicate that *xButyagrus nabonnandii* is neither rare nor infertile. Seed germination rates of *xB. nabonnandii* are low due to seed predation by beetle larvae and seedless fruit production, which is also observed in the genera of the parental species. Furthermore, as in its parents, the morphology of the hybrid is complex, and future anatomical and molecular approaches are important for a better delimitation and understanding of the biology of *xB. nabonnandii*.

Keywords: intergeneric hybrid, morphometry, plant morphology, palm trees, propagation.

Resumo

xButyagrus nabonnandii (Prosch.) Vorster é conhecida como palmeira-mula por ser considerada estéril, apesar de ter sido utilizada com sucesso em retrocruzamentos. O híbrido resulta do cruzamento entre *Syagrus romanzoffiana* (Cham.) Glassman e *Butia odorata* (Barb.Rodr.) Noblick, é tido como raro e possui morfologia pouco estudada. Objetivou-se estudar a morfologia de *xB. nabonnandii* e verificar sua esterilidade através da germinação de suas sementes a partir de diferentes populações naturais. O híbrido foi registrado em quatro municípios sendo, em três desses, de ocorrência inédita. Em um dos municípios visitados, foram contabilizados 20 espécimes. A morfologia vegetativa apresentou menor variação do que a reprodutiva. Entretanto, parte dos caracteres morfológicos vegetativos diferem do descrito na literatura para espécimes cultivados. Nossos dados indicam que além de não ser raro, o híbrido é fértil. As taxas de germinação das sementes de *xB. nabonnandii* são baixas devido à predação das sementes por larvas de besouros, além da produção de frutos sem sementes, o que também ocorre nos gêneros das espécies progenitoras. Além disso, assim como em seus parentais, a morfologia do híbrido é complexa, sendo importantes futuros estudos anatômicos e moleculares para uma melhor delimitação e compreensão da biologia de *xB. nabonnandii*.

Palavras-chave: híbrido intergenérico, morfologia vegetal, morfometria, palmeiras, propagação.

1. Introduction

Hybridization is a natural phenomenon commonly observed in plant species, which can significantly contribute to plant evolution and speciation (Noblick, 2019; Rosa et al., 2021). Often, hybridization favors heterozygosity accompanied by greater hybrid vigor

of plants, expressed in growth and seed production (Glombik et al., 2020). An example of a plant family known for several interspecific and intergeneric natural hybrids is Arecaceae (Glassman, 1971, 1987; Dransfield et al., 2008; Noblick, 2010, 2017; Soares et al., 2014b, a).

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This family is known for its high genetic diversity in tropical and subtropical regions and is of fundamental importance in many forest and savanna ecosystems, offering important resources for herbivores, pollinators, and animals that feed on fruits and seeds (Noblick, 2010; Muscarella et al., 2020).

The Arecaceae have about 2,600 species in 185 genera (Baker and Dransfield, 2016; POWO, 2023). In Brazil, the genera *Butia* (Becc.) Becc. and *Syagrus* Mart. stand out for many endemic and sympatric species, which favors the emergence of rare hybrids within or even between genera, such as *×Butyagrus Vorster* (Glassman, 1971; Noblick, 2010, 2012, 2017; Soares et al., 2014b, a, Engels et al., 2021). Among the intergeneric hybrids, *×Butyagrus nabonnandii* (Prosch.) Vorster was first reported by Proschowsky (1921). Its etymology was a tribute to Paul Nabonnand, who, in the 1890s, was the first to hybridize the parent species in France artificially (Noblick, 2010). However, the first record of natural hybridization dates from the 1940s, when Professor Max Burret from the Berlin Botanical Garden received two photos of a palm tree occurring in Porto Alegre municipality, Rio Grande do Sul State, Brazil. Moreover, there were reports of naturally-occurring specimens in Uruguay (Burret, 1940; Noblick, 2010). As for Brazil, according to Glassman (1971), the hybrid “is thought to be indigenous” from Porto Alegre. In Noblick’s treatment for *Butia*, the Rio Grande do Sul State also appears on the occurrence map of *×B. nabonnandii* but not in the description of the hybrid’s habitat (Noblick, 2010) – perhaps because those were cultivated specimens. Later, the revision of the Arecaceae of Rio Grande do Sul by Soares et al. (2014b) listed and described *×B. nabonnandii* for the municipality of São Vicente do Sul, based on a cultivated specimen.

In addition to *×B. nabonnandii* that originates from the cross between *Butia odorata* (Barb. Rodr.) Noblick and *Syagrus romanzoffiana* (Cham.) Glassman, two other natural intergeneric hybrids between *Syagrus* and *Butia* are also known for the southern region of Brazil. The first is *×Butyagrus alegretensis* K. Soares, derived from *Butia lallemantii* Deble & Marchiori and *S. romanzoffiana* in Rio Grande do Sul (Soares et al., 2014b). The second is the recently described *×Butyagrus paranaensis* Engels, T.A.Meyer & K.Soaes, a cross between *Butia eriospatha* (Mart. ex Drude) Becc. and *S. romanzoffiana* (Engels et al., 2021) in the Paraná State, where the parents are also sympatric (Noblick, 2010, 2017; Soares et al., 2014b).

There are two major gaps in the literature regarding *×B. nabonnandii*. The first concerns its sterility, once the hybrid is considered sterile due to the lack of reports on seed germination (Noblick, 2010; Soares et al., 2014b), giving rise to its popular name, mule palm. However, its pollen was used in backcrosses, including with the genus *Jubaea* (Riffle et al., 2012), which suggests that the hybrid may be fertile. The second gap concerns the descriptions of *×B. nabonnandii*, based on a few cultivated specimens outside their natural area of occurrence with a few samples deposited in herbaria. Thus, a greater collection effort from different populations is justified (Glassman, 1971; Noblick, 2010; Soares et al., 2014b; Noblick and Sant’Anna-Santos, 2021). Furthermore, we hypothesize that this hybrid may naturally present morphologic variation not yet contemplated in previous descriptions.

Studies evaluating germination potential, detailed morphological analysis that includes specimens from different populations, can increase this hybrid’s scientific and technological potential similar to that reported with other palms, such as açai (*Euterpe oleracea* Mart.) (Beghini et al., 2013). Thus, the morphometric analysis of the hybrid’s specimens is essential for providing subsidies for its propagation and conservation. In addition, morphometry allows the detection of inter and intrapopulation phenotypic variations that can be used to infer the genetic variability of individuals and their populations or to estimate speciation events and effects of human action on a given species (Zuffo et al., 2016).

Given the above, this study aimed to evaluate the morphology of specimens from different naturally occurring populations, in addition to the interpopulation phenotypic variation and the germination of *×B. nabonnandii*, to answer the following questions: 1) is *×B. nabonnandii* a rare hybrid? 2) is there significant phenotypic variation between different populations of the hybrid? 3) are wild specimens morphologically different from cultivated ones? 4) to which parent is the hybrid most similar? 5) are their seeds sterile?

2. Material and Methods

The study was carried out in four distinct areas in the Rio Grande do Sul State, Brazil, consisting of typical landscapes of the Pampa biome, including some ecotone regions with the Atlantic Forest biome, in the municipality of Venâncio Aires. The region’s climate is Cfa, humid subtropical, according to the Köppen-Geiger climate classification (Kottek et al., 2006). The morphometric analysis collections included adult and fertile plants of *×B. nabonnandii*, and were carried out in the following municipalities: Venâncio Aires (29°37’08”S, 52°11’40”W; 29°31’26”S, 52°09’25”W; 29°33’05”S, 52°10’05”W), Porto Alegre (30°01’58”S, 51°13’48”W), Cachoeira do Sul (30°02’21”S, 52°53’38”W), and Manoel Viana (29°35’21”S, 55°28’58”W).

The fieldwork was carried out from June 2019 to July 2022 in four spontaneously occurring populations. Six specimens were sampled, and four of them had vouchers deposited in the HBEI Herbarium (New York Botanical Garden, 2023, continuously updated): HBEI1638 (Venâncio Aires); HBEI1642 (Manoel Viana); HBEI1640 (Porto Alegre); HBEI1641 (Cachoeira do Sul). Unfortunately, we could not voucher two specimens due to technical difficulties collecting and herborizing tall individuals with large vegetative and reproductive organs, as Glassman (1970) and Soares et al. (2014b) reported. The two non-herborized specimens did not show significant differences from those in the same area of occurrence.

For the morphometric analysis, fully developed leaves, inflorescences, and infructescences in the ripening stage were collected. For the germination analysis, the seeds were obtained by selecting fruits and removing their pulp according to previous methods (Fior et al., 2018). Therefore, 20 healthy and ripe fruits of each individual were selected (120 in total) for morphometric analysis, morphological characterization, and verification of the presence of seeds.

Then, the fruit pulp was manually removed, the pyrenes were washed in running water, placed on a laboratory bench for drying, and later packed in paper bags and identified for further fractionation.

During seed release, the pyrenes were stored in the shade at room temperature for ten days to favor the extraction of the seeds, which generally remain attached to the endocarp, according to the methodology proposed by Rodrigues et al. (2015) and Santos et al. (2019). The extractions were performed by pressing and breaking the endocarp with a manual hammer. Next, the pyrenes were fixed in a size 3 bench vise and sawed with a 12-inch fine-blade saw. Then, 60 healthy seeds (20 per individual), except for the Venâncio Aires, whose endocarps did not have seeds.

The seeds were placed in moist cotton for 35 days to germinate. Next, the seeds were sown individually 3 cm deep in polypropylene pots with a capacity of 415 ml, containing substrate with a mixture of 1/3 of sand and 2/3 of organic soil (Meerow and Broschat, 1969). They were kept in a greenhouse in 50% shade, with a minimum temperature of 14 °C and a maximum of 26 °C, for 120 days. Irrigation occurred daily, maintaining field capacity. Germination was monitored twice monthly, and after 120 days of seed sowing, the protrusion of the cotyledonary petiole occurred, which was monitored until it reached approximately 1 cm in length (Carvalho et al., 2015).

In the morphometric evaluation, a flexible measuring tape and a digital stainless steel caliper (MTX, China), with a resolution of 0.01 mm, were used to measure the length and width of the vegetative and reproductive structures. The wet mass of fruits, mesocarps, pyrenes, and seeds

was weighed on an analytical digital scale (MH-200, CHJ, China) with a resolution of 0.01 g (Muscarella et al., 2020). The estimation of the number of flowers per inflorescence adopted the methodology of Schwartz et al. (2010). The terminology used for gauging and evaluating the vegetative and reproductive structures of the *x*B. *nabonnandii* specimens evaluated here follow that used in the literature (Dransfield et al., 2008; Glassman, 1971; Noblick, 2010, 2017; Soares et al., 2014b; Sant'Anna-Santos, 2021). The images of the vegetative and reproductive structures were obtained with a digital camera (α 3000 ILCE, Sony, China) with an 18 to 55 mm objective and a 25 mm sensor.

The vegetative morphometric data were assessed among all the municipalities, and the data of the reproductive morphology were measured for each municipality. Two-way analysis of variance (two-way ANOVA) for multiple comparisons was used to analyze quantitative data. Prism GraphPad (version 6.0, GraphPad Software Inc, USA) was used for the analysis and generation of graphs, and the results were presented as mean \pm standard deviation of the mean (MSD), and significant differences were considered when $P < 0.05$.

3. Results

3.1. Occurrence

Hybrid specimens were found in four municipalities in the Rio Grande do Sul State: Cachoeira do Sul, Manoel Viana, Porto Alegre and Venâncio Aires (Figure 1).

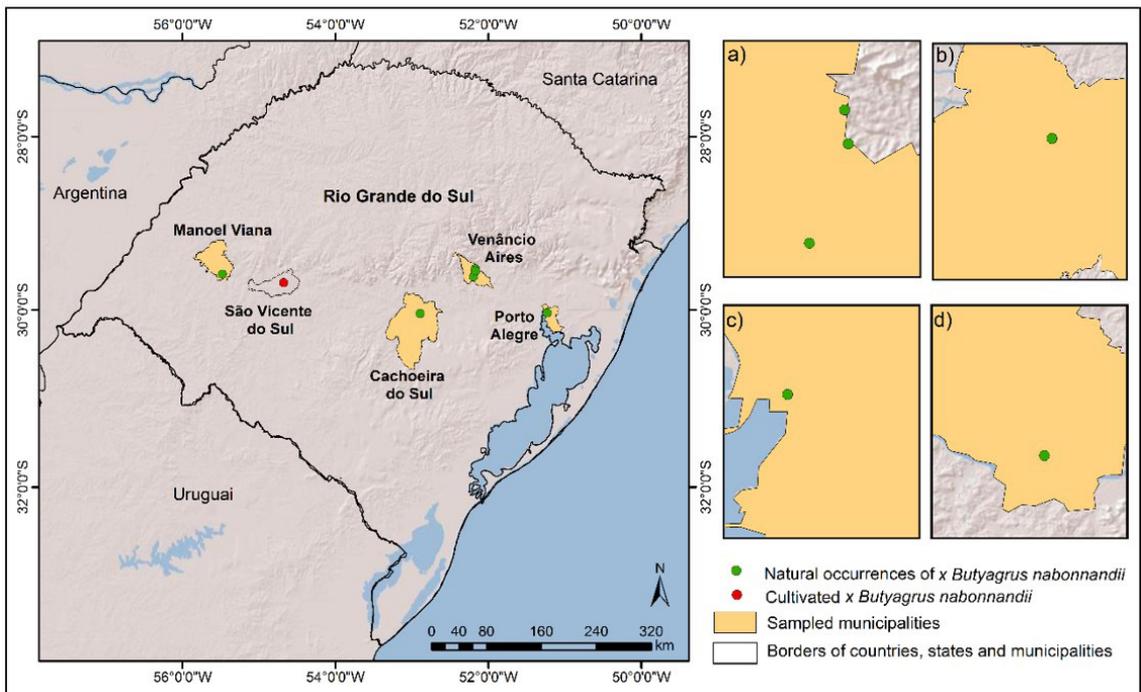


Figure 1. Geographic distribution of *x*B. *nabonnandii* in Brazil. The green dots indicate the collection sites. **a.** Venâncio Aires; **b.** Cachoeira do Sul; **c.** Porto Alegre; **d.** Manoel Viana. The red dot indicates a cultivated specimen in São Vicente do Sul [data retrieved from Soares et al. (2014b)].

In these places, the largest population (20 individuals) was from Venâncio Aires, while in other areas, hybrids occur in small numbers (one or two specimens). In these study areas, hybrid specimens occur sympatrically with their putative parents, especially nearby *B. odorata* (Figure 2a). Flowering was observed throughout the year, mainly between October and February, with an average of one to three inflorescences per individual.

3.2. Vegetative morphometry

Plants are $4.16 \text{ m} \pm 0.70 \text{ m}$ tall, solitary (Figure 2b-2d) with aerial stems, $2.87 \text{ m} \pm 1.1 \times 0.51 \text{ m} \pm 0.1 \text{ m}$. The external texture is generally marked by the semi-persistent leaf sheaths bases, which are encrusted and evenly distributed along the entire stem (Figure 2e).

Leaves are pinnate, $4.78 \pm 0.52 \text{ m}$ long, in number of 15 ± 2 in the crown, slightly arched, and dark green (Figure 2f). Leaf sheaths are $70.04 \pm 5 \text{ cm}$ long, $26 \pm 2 \text{ cm}$ wide, with persistent margins with flexible fibers (Figure 2g). Pseudopetioles are $98 \pm 5 \text{ cm}$ long with flexible dentate margins (Figure 2h). The leaf rachis is $3.10 \pm 0.12 \text{ m}$ long. The first four pairs of pinnae are grouped into the proximal portion of the leaf rachis (Figure 2i). The number of pinnae ranged from 113 to 150 pairs, irregularly (slightly) inserted along each side of the rachis at one or more angles ca. 2 cm apart, with entire margins, linear, ending slightly acuminate, and with asymmetric apex, middle pinnae $84 \pm 2 \times 2.6 \pm 0.48 \text{ cm}$. The midrib is adaxially projected, and the lower vein has ramenta near the rachis (Figure 2j).



Figure 2. Vegetative morphology of $\times B. nabonnandii$. **a-b.** Hybrid (white arrow) cohabiting with one of the parents, *B. odorata* (black arrow); **c.** An individual in Porto Alegre; **d.** An individual in Cachoeira do Sul; **e.** Remnants of the semi-persistent sheaths; **f.** Pinnae irregularly inserted into the leaf rachis; **g.** Detail of the leaf sheath with soft fibers; **h.** Pseudopetiole with dentate margins; **i.** Pinnae inserted in a group in the proximal portion of the leaf rachis; **j.** Ramenta on the abaxial surface of the pinnae (black arrowhead) near the insertion point on the leaf rachis.

3.3. Reproductive morphometry

Peduncular bracts are 1.84 ± 0.38 m long, 23 ± 2 cm wide, acute to acuminate with a beak 12 ± 2 cm long, woody, externally grooved (slightly to deeply), green when closed, and cream-brown when open (Figure 3a-3e). Inflorescences are interfoliar (Figure 3f), 124 ± 20 cm long, rachis 105 ± 5 cm long, and peduncle 35 ± 5 cm long. They are monoecious, protandric hybrids with rimose anthers. The flowers occur in triads, with a pistillate flanked by two staminate flowers (Figure 3g). The arrangement of flowers in triads in the proximal and median portions of the rachillas occupies approximately $2/3$ of the length of the rachilla, while staminate flowers occupy the distal portion. Pistillate flowers have an average width

of 5.65 ± 0.35 mm and an average length of 6.82 ± 0.54 mm, cream color, unilocular ovary, trimerous corolla with imbricate petals (Figure 3h), and trimerous calyx with free sepals. The staminate flowers have an average width of 14.02 ± 0.53 mm and an average length of 11.58 ± 0.59 mm, are cream-colored, and are also trimerous, with free petals, with six stamens (Figure 3h). We observed $24,750 \pm 2000$ staminate flowers and $8,250 \pm 987$ pistillate flowers per inflorescence, resulting in a proportion of three staminate flowers per pistillate flower. The rachillas presented an average length of 56.32 ± 5.34 cm in the proximal portion of the rachis, 43.21 ± 9.89 cm in the middle portion, and 20.1 ± 11.38 cm in the distal portion. The average total number of rachillas was 250 ± 15 .

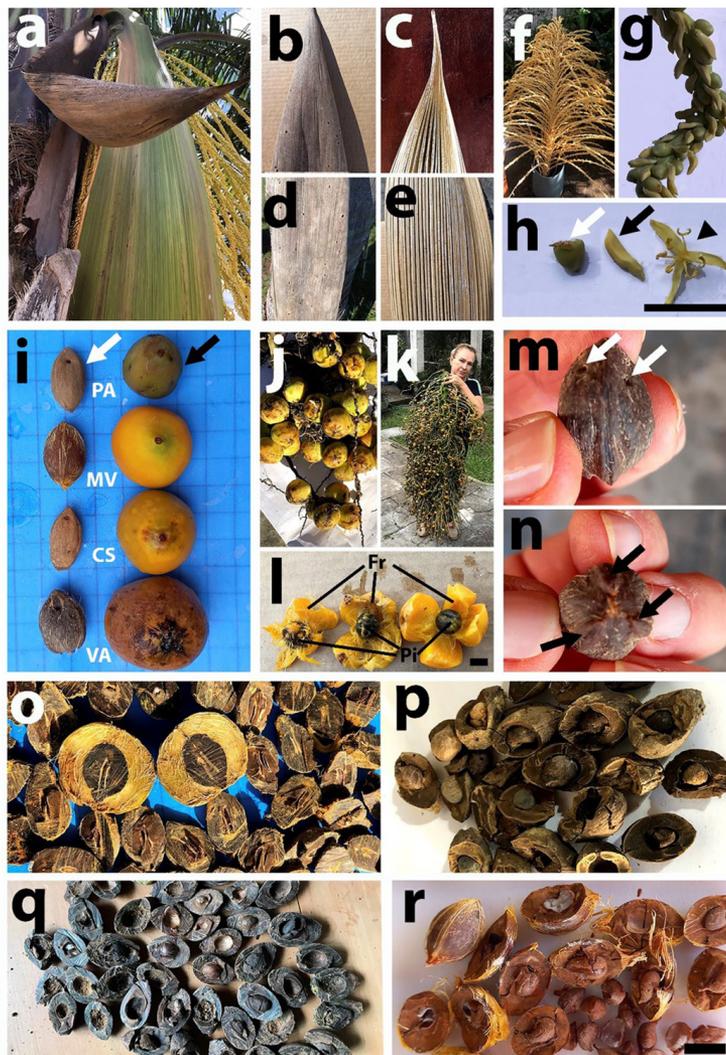


Figure 3. Reproductive morphology of *xB. nabonnandii*. **a.** Peduncular bract externally striated; **b.** Acuminate beak; **c.** Acute beak; **d.** Peduncular bract slightly striated; **e.** Peduncular bract striated; **f.** Paniculate inflorescence; **g.** Fertile rachilla, showing the triads; **h.** Closed pistillate flower (white arrow) and closed (black arrow) and open (arrowhead) staminate flowers; **i.** Pyrenes (white arrow) and fruits (black arrow): Porto Alegre (PA); Manoel Viana (MV); Cachoeira do Sul (CS) and Venâncio Aires (VA); **j-k.** Infructescences of Venâncio Aires and Cachoeira do Sul; **l.** Depulped fruits (fr) with exposed pyrene (pi); **m-n.** Asymmetric subbasal pores of the endocarp (white arrows) with three projections (black arrows) in the apical portion of the endocarp; **o.** Open pyrenes without cavity or seeds (Venâncio Aires); **p-q.** Open pyrenes with and without seeds of individuals from Porto Alegre (**p**) and Cachoeira do Sul (**q**); **r.** Closed and open pyrenes, with and without seeds of the individuals of Manoel Viana. Scale bars: 1 cm.

Fruits are drupes, 23.12 ± 5.63 mm \times 24.1 ± 3.70 mm (equatorial and polar lengths), and have a wet mass of 9.8 ± 4.74 g (Table 1, Figure 4a-4b). The fruits vary from globose to ovoid, are dark green when immature, and yellow to orange when ripe (Figure 3i). In the municipality of Venâncio Aires, the fruits of the hybrids showed a globular shape, yellow color, brown streaks at their apex, and larger dimensions compared to the other municipalities studied (Figure 3i). Fruit maturation occurs irregularly, with immature and ripe fruits observed in the same infructescence (Figure 3j-3k). When ripe, fruit drop

occurs spontaneously. The fruits are edible, consisting of a thin epicarp and a fibrous, mucilaginous, juicy, and sweet mesocarp with one pyrene per fruit (Figure 3l).

The pyrenes, measuring 13.66 ± 0.69 mm \times 21.19 ± 1.51 mm of equatorial and polar length, respectively, and a wet mass of 2.40 ± 0.55 g (Table 1, Figure 4a-4b), are made up of rigid and lignified endocarps. The endocarp has three sub-basal pores, often not symmetrical (Figure 3m). The external endocarp texture is generally smooth and homogeneous, with a light brown color when dry, except for the pyrenes of the fruits of Venâncio Aires individuals,

Table 1. Comparative morpho biometry of *x*B. *nabonnandii* fruits, pyrenes and seeds in four Rio Grande do Sul populations. Descriptive estimates of the mean, maximum (Max), minimum (Min) values and respective standard deviation (SD) and coefficient of variation (CV, %) of the wet fruit mass (WFM), polar fruit length (PFL), equatorial fruit length (EFL), wet pyrene mass (WPM), polar pyrene length (PPL), equatorial pyrene length (EPL), wet seed mass (WSM), polar seed length (PSL) and equatorial seed length (ESL) from 120 fruits/pyrenes/seeds from the municipalities of Venâncio Aires, Porto Alegre, Cachoeira do Sul and Manoel Viana.

Dimension	Mean	Max	Min	SD	CV (%)
WFM (g)	9.85	16.1	4.59	4.74	48.14
PFL (mm)	24.05	27.58	20.29	3.07	12.80
EFL (mm)	23.12	28.47	15.18	5.63	24.35
WPM (g)	2.40	3.03	1.74	0.55	22.96
PPL (mm)	21.19	23.19	19.56	1.50	7.08
EPL (mm)	13.66	14.63	13.14	0.69	5.11
WSM (g)	0.27	0.28	0.26	0.01	3.70
PSL (mm)	10.79	11.08	10.58	0.25	2.31
ESL (mm)	7.30	7.32	7.28	0.02	0.27

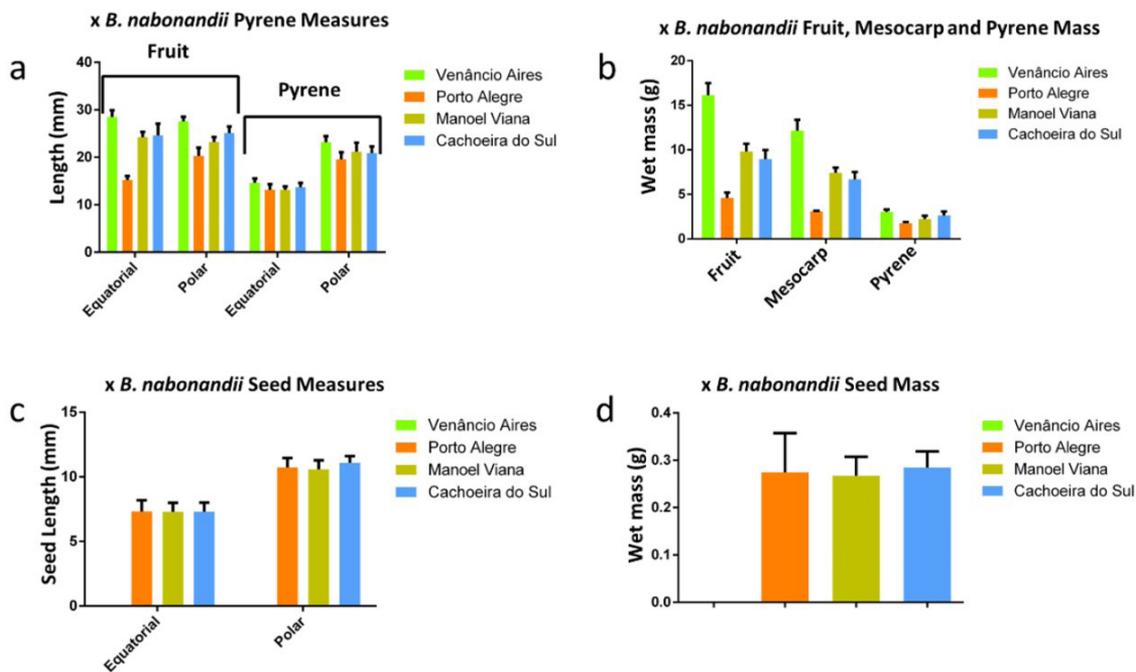


Figure 4. Distributions of measurements and wet mass of fruits, mesocarp, pyrenes, and seeds of *x*B. *nabonnandii* (mean \pm SEM). **a.** Equatorial and polar lengths of the fruits and pyrenes; **b.** Wet mass of fruits, mesocarps, and pyrenes; **c.** Equatorial and polar lengths of the seeds; **d.** Wet mass of the seeds. Venâncio Aires, Porto Alegre, Manoel Viana, and Cachoeira do Sul, Rio Grande do Sul, Brazil.

which presented the external texture of the endocarp marked at the apex by three projections. (Figure 3n). Also, in individuals from Venâncio Aires, all fruits sampled showed massive endocarps with a vestigial cavity lacking seeds (Figure 3o). In fruits from Porto Alegre (Figure 3p), Cachoeira do Sul (Figure 3q), and Manoel Viana (Figure 3r), most endocarps had a cavity with or without seeds.

The smallest equatorial length of the fruit was found in Porto Alegre (Figure 4a), while the greatest polar length was found in Venâncio Aires (Figure 4a). The pyrenes had similar equatorial lengths regardless of the population, but the polar length was slightly higher in Venâncio Aires (Figure 4a). The highest wet mass of fruit and mesocarp was found in Venâncio Aires, while Porto Alegre presented the lowest (Figure 4b). The pyrene wet mass was similar in all populations (Figure 4b).

The seeds presented 7.28 ± 0.02 mm \times 10.79 ± 0.25 mm of equatorial and polar lengths, respectively, and

a wet mass of 0.27 ± 0.01 g (Table 1). They were light to dark brown, ovoid, with a usually prominent operculum (Figure 5a-5c). The equatorial and polar lengths of the seeds (Figure 4c) and their wet mass were similar in the three populations where seeds were found (Figure 4d). In the Porto Alegre population, 44 pyrenes (88%) had seeds, and 11 were intact (12%). The seeds were uniform in size and shape. Infestation by beetle larvae was documented in 24 seeds (Figure 5d-5e), indicating seed vestiges in the endocarps. Furthermore, in six (12%) of the pyrenes examined, no seeds nor obvious cavities were found. In Cachoeira do Sul, 39 pyrenes (78%) had seeds, and 31 were intact and varied in size. Moreover, eight endocarps either had beetle larvae inside or had holes, indicating predation by larvae (Figure 5f). Moreover, six (12%) endocarp cavities had no seeds, and five had vestigial cavities. In Manoel Viana, 47 pyrenes (97%) had seeds of uniform sizes, and three (6%) had only vestiges of cavities.

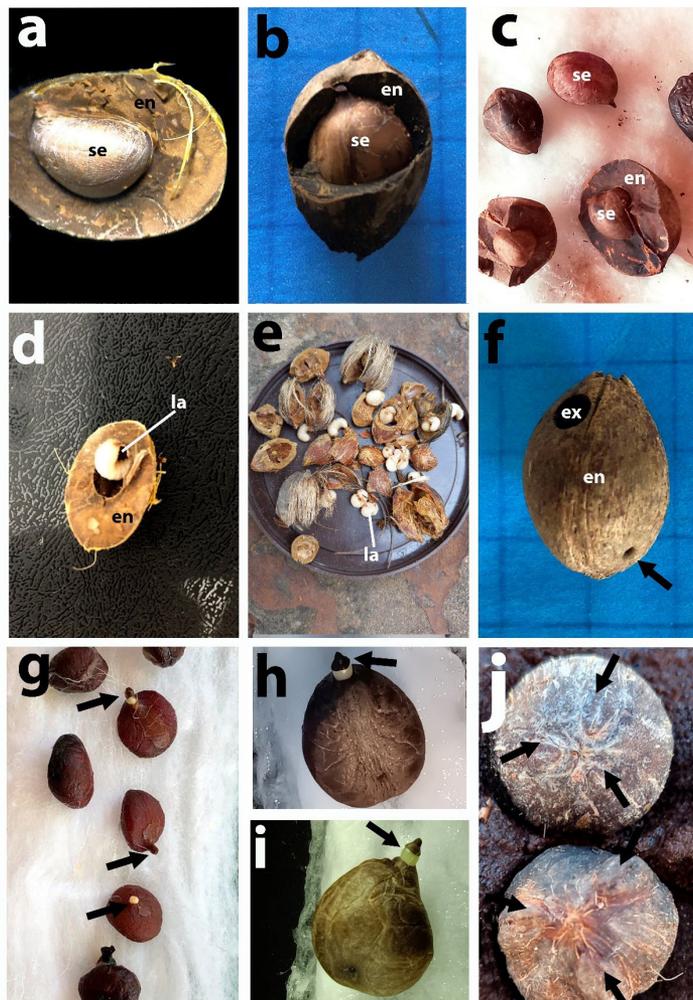


Figure 5. Pyrene morphology of *xB. nabonnandii*. **a-b-c.** Variation of the seed shape (se) in individuals from Porto Alegre (**a**), Cachoeira do Sul (**b**), and Manoel Viana (**c**); **d-e.** Coleopteran larva (la) inside the cavities of the endocarps (en) of the individual from Porto Alegre; **f.** Exit hole (ex) in the endocarp (en): the black arrow indicates one of the subbasal pores of the endocarp; **g-h-i.** Seed germination: the black arrows indicate the protrusion of the cotyledonary petiole; **j.** The arrows indicate projections at the apex of the pyrenes, showing the similarity of *S. romanzoffiana* with specimens of *xB. nabonnandii* from the municipality of Venâncio Aires. Abbreviations: en (endocarp), se (seed).

3.4. Germination

After 160 days, 48 (80%) of the 60 seeds sown did not germinate. From the ungerminated seeds, 32 were rotten, and 16 were withered. Twelve (20%) embryos germinated, emitting the cotyledonary petiole (Figure 5g-5i). The Manoel Viana had a higher germination rate, with five germinated seeds (Figure 5g), while four from Porto Alegre germinated (Figure 5h). Finally, three seeds from Cachoeira do Sul germinated (Figure 5i).

4. Discussion

Our results confirm that *×B. nabonnandii* occurs naturally in the state of Rio Grande do Sul (Glassman, 1971; Noblick, 2010; Soares et al., 2014b). The only specimen previously collected for this hybrid in Brazil was in cultivation in the municipality of São Vicente do Sul (Soares et al., 2014b). Our data also confirm the occurrence of the hybrid in the municipality of Porto Alegre, as previously reported but not collected by Burret (1940). The hybrid was also registered for Pelotas by Lorenzi et al. (2010), page 184, photos 1 and 2. Flora Brasileira: Arecaceae (Palmeiras). Moreover, we added three more municipalities to the occurrence area of the hybrid (all with sampled specimens). Previous reports described only one or two specimens for each occurrence (Glassman, 1971; Soares et al., 2014b), which certainly contributed to characterizing the hybrid as rare. Since we found *×B. nabonnandii* at several sites, with many specimens at least in one of them, the hybrid can no longer be considered rare. In the distribution, the occurrence is possible for where there is sympatry between the parents.

We observed significant vegetative and reproductive variation between our data and the literature for *×B. nabonnandii* (Glassman, 1971; Noblick, 2010; Soares et al., 2014b). Here, we report the number and position of endocarp pores for the first time for the hybrid. Furthermore, the size was significantly smaller in the wild-sampled hybrids than in the cultivated ones reported by Noblick (2010) and Soares et al. (2014b). For *Butia*, there is already a record of a significant change in size in cultivated specimens (Noblick, 2010). The stipe texture seems to be variable in *×B. nabonnandii*. It was encrusted with the semi-persistent bases of the sheaths in the samples we analyzed and a specimen from the Porto Alegre described by Glassman (1971). However, both Noblick (2010) and Soares et al. (2014b) reported that the stipe of *×B. nabonnandii* was smooth. Another contrast between our data and the literature is the number of seeds. We consistently found one seed per endocarp, whereas other authors reported one or two seeds per endocarp (Glassman, 1971; Noblick, 2010; Soares et al., 2014b).

Our morpho-biometric results also indicate considerable variation in reproductive morphology among the four studied areas. However, the characters that varied the most are commonly variable in Arecaceae species due to environmental factors associated with genetic variability (Mhanhmad et al., 2011). Recently, Noblick and Sant'Anna-Santos (2021) also indicated that characters of leaf morphology and anatomy, considered stable for *Butia*

species (Sant'Anna-Santos et al., 2015, 2018) and *Syagrus* (Noblick, 2017b), could vary according to different growing conditions or the population analyzed. This corroborates the high morphological diversity of taxa of recognized complexity, such as *Butia* and *Syagrus*. Thus, in such cases is essential to sample across the entire distribution of a given species. Distinct individuals of hybrid origin are expected to have great variation (mainly intergeneric), fixing both heterozygosity and new hybrid characters (Chen, 2010).

In cultivation, *×B. nabonnandii* is the result of transferring the pollen grains of *S. romanzoffiana* to the receptive stigmas of *Butia odorata* (Noblick, 2010; Rosa et al., 2021). Taking into account anemophilous pollination, according to Oliveira et al. (2002), under natural conditions, *B. odorata* could be the female progenitor since this species is smaller than *S. romanzoffiana* (Noblick, 2010, 2017). Moreover, *S. romanzoffiana* is also recognized for its higher pollen production (Begnini et al., 2013). Therefore, the highest probability of successful airborne pollination is a taller specimen with a higher production of pollen, as many are lost in the environment (Dransfield et al., 2008). In addition, *B. odorata*, in all studied localities, is more commonly observed in the vicinity of hybrid specimens than *S. romanzoffiana*.

Interestingly, Venâncio Aires presented morphological characters significantly different, such as the absence of seeds and protrusions in the apical portion of the endocarp and a larger number of individuals. Therefore, besides phenotypic variation, another hypothesis for the uniqueness of Venâncio Aires hybrids could be an inverted paternity, i.e., *B. odorata* as the male and *S. romanzoffiana* as the female parent. However, as hybridization involves complex extrinsic and intrinsic factors, morphology alone cannot definitively indicate the male and female parents of the naturally-occurring *×B. nabonnandii*. Therefore, future efforts should focus on controlled crossings and applying molecular biology techniques to better assess the variation according to the localities studied.

Concerning seed viability, both Noblick (2010) and Soares et al. (2014b) stated that the hybrid is sterile since its seeds do not germinate. However, in all sites where seeds were found, we observed germination after 160 days of sowing. Moreover, the germination rate was similar to that observed for species of *Butia* (Carpenter, 1988), indicating that this hybrid is fertile.

In this work, seedling stage development was not followed. According to the literature, for most palm trees, the time required for the emergence of the seedling is about two years (Waldow et al., 2013). In this regard, new studies are indicated to monitor the development of this hybrid in including studies with effects of climate and vegetation structure on palm (Hilário and Toledo, 2016).

According to Tomlinson (1990), more than 25% of all palm species require more than 100 days to germinate and present less than 20% of total germination. These data corroborate data from other studies (Meerow and Broschat, 1969; Hoffmann et al., 2014), indicating that palm species have low and non-uniform germination. Moreover, intrinsic and extrinsic factors influence the low percentage of germination of palm seeds, including the climate and parasite infestation (Pivetta et al., 2005).

Thus, studies evaluating seed fate in the field can help to elucidate the effects of habitat disturbance on the vital growth and survival rates of individuals and on the long-term persistence of populations (Ferreira et al., 2022).

Furthermore, it should be taken into account that the hybrid has sexual reproduction that occurs in sympatry with its parents, such factors can influence the origin of pollen from both parents in fertilization and seed production (Oliveira et al., 2002; Rivas and Barilani, 2004). In our study, it was not possible to identify which parent provided the pollen for hybrid formation. Complementary molecular biology studies would be necessary to assess pollen and ovule sources in order to determine if x*B. nabonnandii* hybridization is unidirectional or if it can occur in both directions.

Therefore, seed predation by beetle larvae likely decreases the germination rate of x*B. nabonnandii*. These larvae feed on the endosperms of the hybrid, as reported for its parents and other species of both genera (Sant'Anna-Santos, 2021). Conversely, we found higher germination rates in Manoel Viana, the only place where beetle larvae were absent. In addition to predation, seed dormancy might also affect germination rates. For instance, morphological and physiological dormancy of embryos is attributed to *Arecaceae* (Baskin and Baskin, 2004). However, according to Magalhães et al. (2013), the embryonic structure of *B. capitata* does not limit seed germination, as the dormancy is of a non-deep physiological type.

Here we showed that x*B. nabonnandii* occurs naturally not only in Porto Alegre, as previously reported, but at least in three more localities in Rio Grande do Sul State. In addition, the hybrid can produce viable seeds and form sizeable populations. These results indicate that this hybrid is not rare but more common and even fertile in nature. Significant phenotypic variation exists between different wild hybrid populations and between them and cultivated individuals. In addition, our study presents new morphological descriptors for this hybrid, such as the presence of ramenta and the endocarp pores' position. Morphologically, x*B. nabonnandii* is more similar vegetatively to *B. odorata* and reproductively to *S. romanzoffiana*, although further studies are needed to clarify the paternity of these natural populations. Finally, our findings, including fruit size, presence or absence of seeds, and germination, lay a foundation for management, conservation, and use programs for this palm tree as a food, landscape, and economic resource.

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