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REVIEW ARTICLE

Acrocomia spp.: neglected crop, ballyhooed multipurpose palm or fit for the bioeconomy? A review

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Abstract

Acrocomia spp., a genus of wild-growing palms in the neotropics, is rapidly gaining interest as a promising multipurpose crop. Diverse products can be derived from various components of the palm, the oils being of highest interest. Acrocomia shows similar oil yield and fatty acid composition to the African oil palm (*Elaeis guineensis*). It is, however, able to cope with a wider range of environmental conditions, including temporary water scarcity and lower temperatures, thus potentially a more sustainable alternative to its tropical counterpart. Acrocomia's research history is recent compared to other traditional crops and thus knowledge gaps, uncertainty, and challenges need to be addressed. This review attempts to assess the acrocomia's preparedness for cultivation by highlighting the state-of-the-art in research and identifying research gaps. Based on a systematic literature search following a value web approach, it (a) provides a comprehensive overview of research topics, (b) shows the development of publication activities over time and the drivers of this development, and (c) compiles main findings to assess the acrocomia's preparedness for commercial cultivation. Our results confirm its multipurpose characteristic as a potential feedstock for manifold sectors. Research has continued to increase over the last decade, especially on *A. aculeata* and is driven by the interest in bioenergy. Increasing knowledge on botany has contributed to understanding the genetic diversity and genus-specific biology. This has enabled applied research on seed germination and propagation toward domestication and initial plantation activities, mostly in Brazil. Main research gaps are associated with genotype–environment interaction, planting material, crop management, and sustainable cropping systems. Overall, we conclude that acrocomia is at an early phase of development as an alternative and multipurpose crop and its up-scaling requires the integration of sustainability strategies tailored to location-based social-ecological conditions.

Keywords *Acrocomia aculeata* · Agroforestry · Biodiversity · Bioeconomy · Bio-based value chain · Bio-based value web · Biorefinery · Macaúba · Macaw palm · Coyol · Mbokajá · Minor crop · Oil crop · Vegetable oil

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1 Introduction

Over the last decade, the concept of bioeconomy has emerged in political and research agendas as a pathway to a sustainable transition toward low-carbon societies and the transformation from a fossil-based economy to a knowledge- and bio-based economy, built on renewable biological resources (Birner 2018). The bioeconomy depends on a sustainable biomass supply and thus involves issues related to land use, preservation of biodiversity, as well as climate and environmental protection. These global topics pose challenges for the agricultural and industrial sectors producing food, feed, fibers, fuels, and materials. To date, public interest and demand for alternative crops—in line with the idea of agricultural diversification in the bioeconomy—has been limited to a small number of minor crops including *Jatropha curcas*, *Chenopodium quinoa*, *Salvia hispanica*, *Ananas lucidus*, and *Miscanthus x giganteus*. The reason for this is that the sustainable introduction and establishment of minor crops require comprehensive research and involve numerous risks (Clifton-Brown et al. 2019). In the case of jatropha, e.g., the failure to use a holistic approach resulted in failed expectations and hindered its successful cultivation and marketing, leaving behind negative experiences (Nygaard & Bolwig 2018; Soto et al. 2018). Feasibility studies were not conducted in advance, local growing conditions were overlooked, and the introduction of the crop was characterized by conflicting goals and structural barriers for farmers. Seen in this light, acrocomia is considered a novel prospective minor crop with high-potential products, including edible fruits for human consumption (flour and nuts), animal feed (crushed fruits, press cake, palm leaves), oils (biofuel, cosmetics, nutrition), as well as products for the pharmaceutical and chemical sector (Cardoso et al. 2017; César et al. 2015; Colombo et al. 2018; Hilger et al. 2015) (Fig. 1; Table 1). By implementing holistic approaches and considering lessons learned from other minor and novel crops, the introduction of acrocomia-based value chains could potentially be successful from the outset.

So far, research on acrocomia has mainly addressed individual scientific fields of biomass production or (pre-)processing and products. To the authors' best knowledge, no review of acrocomia research exists to date from a value web perspective, focusing on the acrocomia's preparedness for cultivation. With this goal in mind, we developed a systematic literature review with a detailed categorization of publications and a deep analysis and structuring of findings. In this way, our novel approach adds further information and reveals key research gaps, complementing other reviews on specific topics (de Lima et al. 2018), non-systematic reviews (Hernández 2016), and bibliometric studies (Ampese et al. 2021). The main objective of this

Fig. 1 *Acrocomia totai* in Paraguay, **a** Progeny; **b** plantlet; **c** wild palm; **d** wild palms in open savannahs; **e** farmers collecting fruits; **f** acrocomia fruit bunches; **g** ripe fruits of different sizes from wild palms and fruit composition; **h** pulp and kernel oil samples; **i** marketed edible oils; **j** soaps produced with acrocomia oils; **k** pulp flour, activated carbon from endocarp and by-products (husk and endocarp for combustion and press cakes for natural nutrition) (photographs by the authors).

Table 1 Acrocomia's curriculum vitae.

Distribution	*Acrocomia* is a genus that belongs to the family Arecaceae (palms) and occurs in both the tropics and subtropics including transition areas to the warm temperate latitudes (30° north and south of the equator) from Mexico to the north of Argentina (Cardoso et al. 2017; Henderson et al. 1995; Plath et al. 2016)
Genetic variability	There is evidence of high genetic variability both within and between populations. Although the current number of existing species within the genus *Acrocomia* is still unknown, *A. aculeata* has been found to be the most common species. Variability among naturally occurring genotypes of *Acrocomia*, however, leads to variations in the composition of plant components and physical characteristics (Cardoso et al. 2017; Crocomo & Melo 1996; da Conceição et al. 2015; Henderson et al. 1995; Vianna 2017). Nine *Acrocomia* species have so far been identified (de Lima et al. 2018): ***A. aculeata:*** Neotropics in savannahs ***A. corumbaensis:*** Western border of the Pantanal—Brazil ***A. crispa:*** Cuba ***A. emensis:*** Dwarf species in the Cerrado areas of Brazil (Goiás, Mato Grosso do Sul, Minas Gerais, São Paulo, and Paraná) ***A. glaucescens:*** Acaulescent species in the Cerrado areas of Brazil (Goiás, Mato Grosso do Sul) ***A. intumescens:*** Brazilian Northeast ***A. hassleri:*** Acaulescent species in the Cerrado areas of Brazil and Paraguay (Gauto et al., 2011) ***A. media:*** Puerto Rico ***A. totai:*** Pantanal (Brazil), Paraguayan-Bolivian Chaco, eastern Paraguay (Gauto et al., 2011), north Argentina A list of synonyms of *A. Aculeata* is summarized in de Lima et al., (2018)
Ecophysiological conditions	The palm grows in semi-arid, sub-humid, and humid climates of the Americas in areas with high solar radiation and can cope with dry periods. *A. aculeata* is adapted to seasonal rainfall between (500-) 1000 and 2000 (-3000) mm (Falasca et al. 2017; Plath et al. 2016; Resende et al. 2020), temperatures from 15 to 35 °C, and low elevations ranging from 150 to 1000 m altitude, although there are populations found at 1200 m in the Colombian Andes (Cardoso et al. 2017; César et al. 2015; da Motta et al. 2002; Henderson et al. 1995; Manfio et al. 2011; Markley 1955)
	Single palms as well as dense populations can be found on various soil types and biomes, being more abundant in dry areas and on clayey and eutroferric soils, although acrocomia also grows on sandy soils with low fertility. This includes sandy soil open vegetation, coastal and open savannahs, woodlands, and also disturbed areas like secondary forests and degraded grasslands (Balslev et al. 2011; Cardoso et al. 2017; Henderson et al. 1995; Kahn & de Granville 1992; Machado et al. 2016)
Reproduction	Acrocomia is a monoecious plant, with flowering occurring annually and seasonally with a peak from November to March. It bears unisexual flowers of both sexes arranged in the same inflorescence. Fruits start ripening around twelve months after fertilization (Colombo et al. 2018; de Lima et al. 2018; Mazzottini-dos-Santos et al. 2015a, b; Montoya et al. 2016)
Fruits	Abundant fruits (estimated productivity of 25.5–57.8 kg per adult palm tree of *A. aculeata* (Ciconini et al. 2013; Evaristo et al., (2018)) are produced annually. They are globose, nearly spherical, and edible drupes of 3−5 cm diameter that consist of epicarp (hull), a mucilaginous and fibrous mesocarp (pulp), and a lignified endocarp containing the seed (kernel) (Colombo et al. 2018; Markley 1955; Montoya et al. 2016; Rosado et al. 2019)
Uses	Local communities use fruits, roots, leaves, and stem of acrocomia in manifold artisanal and industrial forms (Balick 1990; Costa et al. 2018a; Lorenzi & Negrelle 2006; Plath et al. 2016; Colombo et al. 2018), the oil-bearing fruits being the most valuable part, as has been documented for Paraguay since the 1950's (Markley 1955). This is mainly due to high oil contents in mesocarp and seed, fatty acid profiles, desirable components of the mesocarp and epicarp (e.g., carotenoids and tocopherols), protein and fiber content, and high fruit yields (Colombo et al. 2018; Schex et al. 2018)
Domestication	Acrocomia is still an undomesticated crop and its use is based mainly on the collection of fruits from natural populations (Cardoso et al. 2017). Acrocomia can be potentially cultivated in agroforestry systems (César et al. 2015). The establishment of acrocomia value chains based on commercially managed plantations is at an early stage of development, as most existing plants still occur in the wild (Plath et al. 2016). To date, the cultivation of acrocomia in initial plantation trials by industry and research institutes, as well as the development of acrocomia-based value chains and marketing is most advanced in Paraguay and Brazil (Colombo et al. 2018; Plath et al. 2016)

review is thus to provide readers with the state-of-the-art of acrocomia research by evaluating the past four decades of published literature and to systematically identify progress and obstacles in implementing acrocomia as a sustainable, alternative multipurpose crop in Latin America. Our focus lies on the primary production of biomass as the basis for developing acrocomia-based value webs. The concept of the biomass-based value web is described by various scholars in the context of the bioeconomy (Birner 2018; Lewandowski 2015; Viaggi 2018; Virchow et al. 2016; Zörb et al. 2018). It provides a web perspective encompassing the interlinkage of various value chains that result from the multiple uses of a given biomass, in this case, acrocomia. The biomass-based value web concept is applied as a holistic framework in this review paper to analyze the scientific literature on acrocomia and extract findings at a fundamental and applied level. This includes the identification of efforts, drivers, potential stumbling blocks, as well as research gaps and needs for its successful implementation as a sustainable and viable feedstock for further multipurpose applications, primarily oil production. For this purpose, peer-reviewed research articles on acrocomia were selected and quantified based on predefined research levels (fundamental or applied) and research from the seeds to advanced applications. Following a value web approach, the evolution of acrocomia studies over time is analyzed to provide insights into the progress, trends, and drivers of research and development. Consequently, major milestones and research needs in regard to primary production of biomass are identified, centered on the question "what is the acrocomia's preparedness for cultivation?"

2 Materials and methods

2.1 Data collection and analysis

This review is based on literature retrieved from the Scopus database. The following search logic was used, including the genus name of *Acrocomia* and vernacular names: Acrocomia OR Macaw palm OR Mbokaya OR Coyol OR Macauba OR Macaúba OR Palma de corozo.

These terms were searched for in publication titles, abstracts, and keywords using a self-developed algorithm built on R (R Core Team 2019) and Bibliometrix (Aria & Cuccurullo 2017). After a first run, it was found that the Scopus database covered all articles also retrieved from Web of Science. With Lattes Platform (Brazilian information system of science and technology), only those articles published on Scopus-indexed journals were retrieved. As the aim was international coverage, the decision was made to collect scientific literature solely from the Scopus database.

Full manuscripts of selected references were obtained from online sources, cross-checked with Lattes. Duplications were removed and manual classification was applied to align the content of the documents with the purpose of this article. A two-tiered and iterative classification process was developed and applied to the screening of retrieved publications. The preliminary classification resulted in the publications being grouped into two categories: fundamental and applied research. The first category corresponds to publications that provide primary knowledge on acrocomia. Publications that provide insights into acrocomia value chains are classified as applied research. Studies found to be outside the scope of this review were excluded. Scientific literature categorized as applied research was further divided into the subcategories: (1) biomass production; (2) processing and products; and (3) sustainability. This categorization was then refined by considering the actual content of abstracts, keywords, and conclusions. As many of the publications covered more than one topic respecting acrocomia, the classification was based on their main focus. This led to an expanded bio-based value web structure, with various topics being covered within the different areas and categories. Publications classified into botanic studies (fundamental research) and biomass production areas (applied research) were in-depth analyzed to assess the progress on the acrocomia's preparedness for cultivation, from genetic characterization through to initial plantations.

3 What do we know about acrocomia so far?

3.1 Categorization of the published literature

Acrocomia research covers a wide range of topics and involves various disciplines. Using the defined search query until 2018, a total of 366 publications were identified. Of these, 15 publications were considered not relevant and subsequently excluded. The remaining publications of the first search ($n=351$) and the newest publications from 2019 until June 2020 ($n=69$) were subdivided into fundamental and applied research following a value web perspective (Fig. 2).

Publications categorized as 'fundamental research' ($n=108$) were found to mainly focus on the genus *Acrocomia* and its interaction with other organisms. They embrace studies related to botany ($n=77$), ethnobotany ($n=18$), and human health risks ($n=13$). Publications in the category 'applied research' ($n=313$) were subdivided into biomass production ($n=64$), processing and products ($n=239$), and sustainability ($n=9$).

Biomass or crop production ($n=64$) refers to publications on the establishment of agricultural production systems, including plant propagation ($n=35$), plant breeding ($n=7$), cultivation systems ($n=7$), harvesting ($n=7$), modeling of acrocomia production and agroclimatic areas ($n=4$), plant nutrition ($n=1$), and plant protection ($n=3$). Publications on processing and products included (pre-)processing methods ($n=34$), application of acrocomia fruits and other plant components as animal feed ($n=21$), bioenergy in the form of liquid and solid energy carriers ($n=87$), human health and nutrition ($n=58$), materials and chemicals ($n=34$), and general publications providing a value chain perspective ($n=5$). Publications addressing sustainability were found to focus on environmental impacts ($n=4$), environmental-economic assessment ($n=2$), social aspects ($n=2$), and socio-economic issues ($n=1$). Bioenergy is addressed in 20.7% of publications on both fundamental and applied research topics. A significant number of publications ($n=68$),

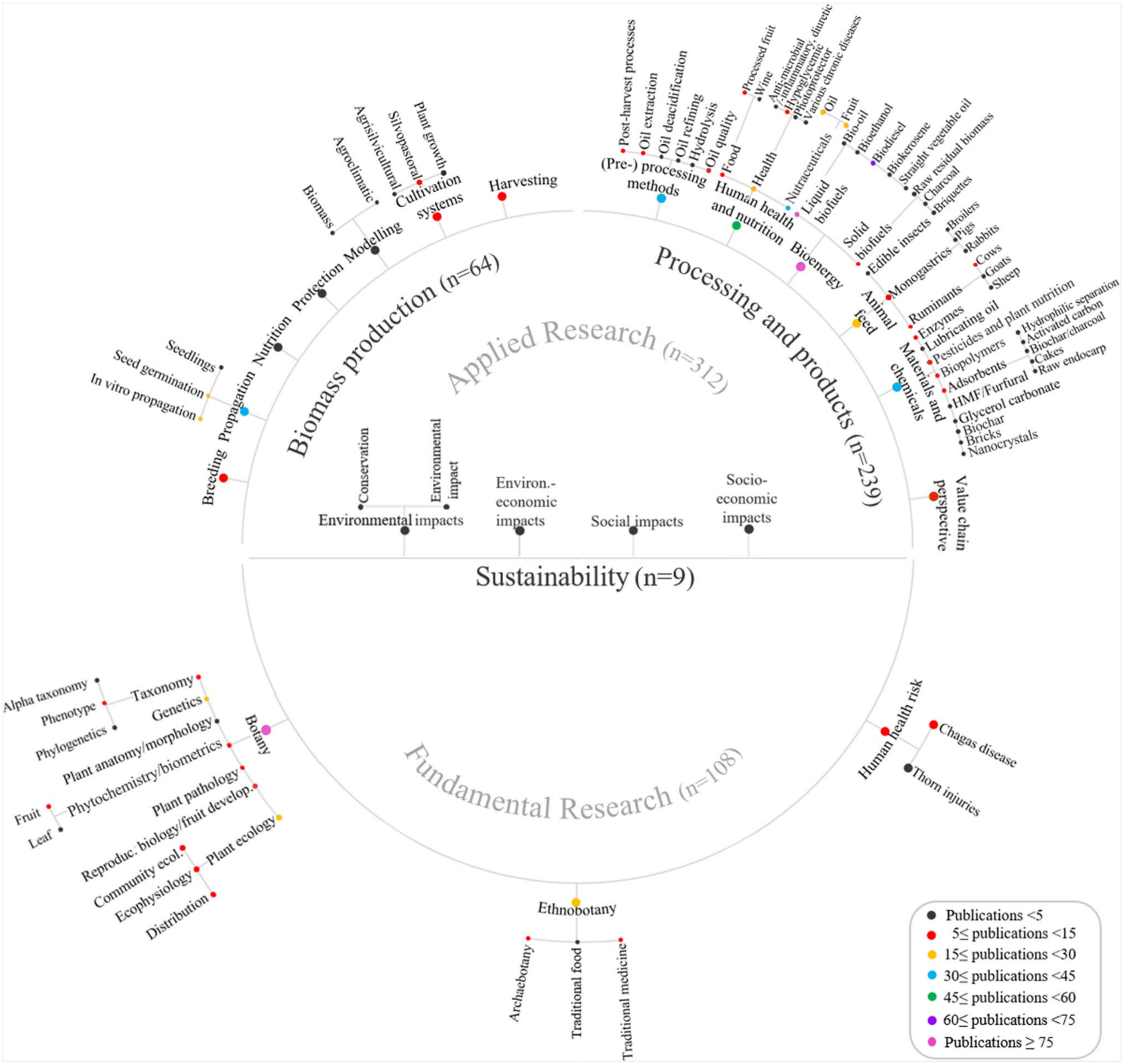

Fig. 2 Dendrogram of acrocomia-related fundamental and applied research topics following a value web perspective.

representing 16.2% of the literature reviewed, addressed biodiesel production from acrocomia oils.

3.2 A short history of acrocomia research

Acrocomia research was initiated in 1763 with a first genus classification (de Lima et al. 2018) and its description in 'Historia naturalis Palmarum' (von Martius, 1824). In the literature retrieved from the Scopus database, the first publication dates back to 1878 with information about the genus *Acrocomia* in Colombia (Posada-Arango 1878) as shown in Fig. 3. However, it was not mentioned again until 1951 when its kernel extracts were reported as a potential pesticide against the tobacco mosaic virus (Lucardie 1951). In regard to its taxonomy, a study was published in 1960 describing the phenotype and structure of acrocomia fruits (Vaughan 1960). From 1951 to 1980, little was published, with the exception of two milestones, indicating the onset of research on the industrial use of acrocomia oil: A study, published in 1955 described the value chain from *A. totai* in Paraguay and fruits (Markley 1955) and a study from 1968 reported on the fatty acid compositions of both the kernel and pulp oil (Landmann & Frampton 1968). During the next 20 years, research diversified into various topics including

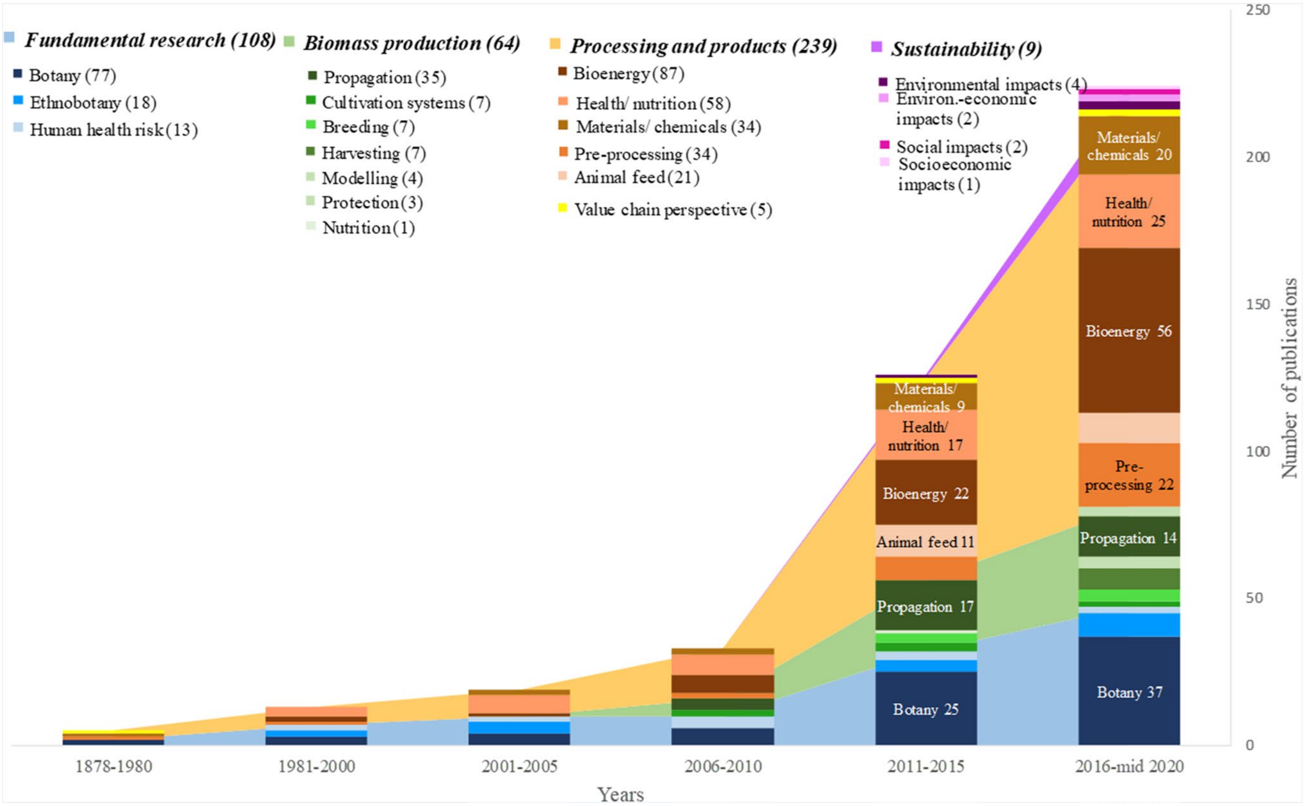

Fig. 3 Evolution of acrocomia-related research topics over time.

reproductive biology, plant pathology, archeobotany, human health risks, and processing and products. At the beginning of the 1980s, e.g., first reports on human health risks were published, revealing acrocomia as one of several palm species that host the Chagas' disease vector (Diotaiuti & Dias 1984; Miles et al. 1983). Since then, acrocomia has been investigated as a potential natural habitat of triatomine bugs, such as the genera *Rhodnius*, which are one of the most common vectors of the parasite *Trypanosoma cruzi* (Diotaiuti & Dias 1984; Longa & Scorza 2005). At the end of this decade, first publications on carotenoids and provitamin A composition of processed fruits appeared, indicating acrocomia's importance from a human nutrition perspective (Hiane & Penteado 1989a). Around the same time, research on postharvest aspects emerged, assessing changes in carotenoid composition in fruits during cold storage (Hiane & Penteado 1989b). In the early 1990s, its reproductive biology and phenology were first described (Scariot et al. 1991, 1995). Later, ethnobotanical studies revealed acrocomia as an important natural resource of the ancient Mayan civilizations that used various palm parts for diverse applications like construction, food, and traditional medicine (Mckillop 1994; Powis et al. 1999). At the end of this decade, acrocomia evolved from its application in traditional medicine to its potential for the human health industry, as new hypoglycemic properties from "coyolosa," a root extract, were discovered (G. Pérez et al. 1997). During this period, pyrolysis of oils was introduced, bringing attention to their potential as biofuels (Fortes & Baugh 1994, 1999) and laying the foundation for the development of bioenergy products like bio-oil.

From 2001 to 2005, new topics related to acrocomia's geographical distribution (da Motta et al. 2002), its association with species of *Eriophyoid* mites (Navia & Flechtmann 2002, 2003), and seed predation (Ramos et al. 2001) were explored. Simultaneously, research on health and nutrition emerged, including studies on (Haines 2004b, 2004a) coyolosa's hypoglycemic properties (Andrade-Cetto & Heinrich 2005; Haines 2004b, 2004a; Hernandez-Galicia et al. 2002) and acrocomia oil's characterization and nutraceutical potential (Belén-Camacho et al. 2005; Bereau et al. 2003). Also new pyrolysis processes were applied to acrocomia oils, fruits, and seed shells to obtain new chemical materials like activated carbon adsorbents (Fortes & Baugh 2004; Jeanne-Rose et al. 2003; Ouensanga et al. 2003). Ethnobotanical studies on the uses of acrocomia in traditional medicine were also published during this period.

From 2006 to 2010, the number of publications on acrocomia increased for two reasons: (i) the increasing interest and research in bioenergy and (ii) breakthroughs in acrocomia research related to agricultural and biomass production.

A milestone during this period was a publication on acrocomia genetics, which established the background for population genetics studies. It characterized eight microsatellite markers to provide information for future species conservation and plant breeding (Nucci et al. 2008). Processing and products research continued to develop through further research on nutraceutical properties of the acrocomia fruit and the introduction of new topics in the areas of preprocessing, bioenergy, and chemical materials. Emerging studies on oil extraction from fruits (Arveláez et al. 2008) and refining (Hernández et al. 2007) were published, followed by the development of novel bio-based products such as plasticizers and biodegradable polymers (Schlemmer & Sales 2010). Furthermore, several studies on alternative bioenergies emerged introducing new liquid and solid biofuel products. The use of straight acrocomia oil as a liquid biofuel was suggested as an alternative to small-scale electricity generation in rural areas (Rodrigues et al. 2009; Xavier et al. 2009). Alternative enzymatic and solid catalysts were used for biodiesel synthesis and production (Alves et al. 2010; Nogueira et al. 2010). The production of charcoal from fruit residues was proposed as a renewable solid biofuel (Boas et al. 2010). Since 2008, biomass production research has gained importance, with the first publication indicating that silvopastoral systems could be suitable options for acrocomia cultivation (Villanueva et al. 2008). The lack of plantlets (due to challenges in propagation) led to the development of first in vitro propagation protocols for the induction of somatic embryogenesis (Luis & Scherwinski-Pereira 2014; Moura et al. 2009), a patent for an acrocomia seed germination protocol (Motoike et al. 2007), and a tetrazolium test to indicate seed germination (Ribeiro et al. 2010). The sporadic emergence of applied agricultural research can be explained by the Brazilian governmental policies to stimulate the cultivation of acrocomia as a potential source of bioenergy products (Lanes et al. 2014).

From 2011 to 2015, initial studies on phylogenetic aspects of acrocomia were published. These revealed new evidence in relation to its taxonomic classification (Eiserhardt et al. 2011; Ludeña et al. 2011), floral structure, and fruit development (Mazzottini-dos-Santos et al. 2015a, 2015b; Montoya et al. 2016). Findings were published for assisting future plant breeding programs, including a study on the biometric and phytochemical traits of fruits and oils (Ciconini et al. 2013). They also included studies on the photosynthetic capacity of acrocomia (Pires et al. 2013) as well as microbial and chemical changes in soils of acrocomia habitats (Diniz et al. 2014). A major advancement in the context of molecular biology was the development of a protocol for DNA extraction from different tissues (Lanes et al. 2013) and cross-species amplification of microsatellite markers for *A. aculeata* (Mengistu et. al. 2016a). In respect to agriculture and biomass production, publications focused on propagation, i.e., in vitro embryogenesis and seed germination protocols. Seed dormancy was confirmed to be the most limiting factor for propagation (Ribeiro et al. 2011). Success in seedling production using pre-germinated seeds emphasized the need to achieve uniform planting material through breeding (Costa et al. 2014). Moreover, plant breeding studies helped to identify new genetic parameters and biometric characteristics required to assess the diversity of progenies and assist in the selection of acrocomia (Berton et al. 2013; Domiciano et al. 2015; Manfio et al. 2011). Indications for extracting oil (post-harvest processes, oil pressing, refining and deacidification) were provided (Ciconini et al. 2013; Mariano et al. 2011; Nunes et al., 2015). Knowledge was gained on enzymatic hydrolysis of oils (Raspe et al. 2013) and new residual products from industrial biodiesel synthesis, such as substrates for the adsorption of industrial dyes (Vieira et al. 2012) and production of microbial enzymes (Souza et al. 2015). Another potential application of acrocomia emerged during this period: animal feed products. Studies focused on the performance and ingestion behavior of ruminants, i.e., goats (Rufino et al. 2011), lambs (da Fonseca et al. 2012), and dairy cows (Azevedo et al. 2013). In human health and nutrition, first reports on diuretic and anti-inflammatory effects of acrocomia oil were released (Lescano et al. 2015a). Respecting bioenergy, research focused on the synthesis of acrocomia biodiesel, its physicochemical characterization, as well as potential and economic perspectives (Aguieiras et al. 2014; Basso et al. 2013; Bressani et al. 2015; Carvalho et al. 2013; Lopes et al. 2013; Navarro-Díaz et al. 2014). Since 2013, research has also covered bioethanol production (Gonçalves et al. 2013). From a value chain perspective, the prospects of using acrocomia as biodiesel feedstock were emphasized, driving the implementation of acrocomia as a non-food crop species (César et al. 2015). The first publication addressing sustainability aspects of acrocomia production was published in de Medeiros et al. (2011). Here, conservation and environmental strategies for the use of acrocomia wood were suggested and its impacts on forested areas discussed.

From 2016 to 2018, published research focused on the development of new techniques to estimate biometric characteristics of acrocomia fruits, such as volume and maturation (Costa et al. 2016). The latter is crucial for the determination of appropriate harvest time. In addition, the need for mechanization of the harvest to reduce labor costs and time promoted new solutions including a semi-mechanized harvesting system based on mechanical vibrations and harvesting machines adapted to acrocomia's fruit-rachilla system (Grupioni et al. 2018; Velloso et al. 2017; Villar et al. 2017). New insights into the genetics and environmental adaptation of acrocomia were elucidated by sequencing and characterizing the complete plastome of *A. aculeata* (Lopes et al. 2018). Soil chemical fertility, particle size, and soil drainage were identified as highly important non-biotic factors impacting size and weight of fruits (Coelho et al. 2017). In Falasca et al. (2017) and Plath et al. (2016), modeling approaches were tested for the first time to delimit potential acrocomia cultivation areas under future climate conditions. Moreover, a first agroforestry system study was published, which proposed alley cropping of coffee and acrocomia to mitigate climate change effects on coffee production (Moreira et al. 2018). Great advances in knowledge regarding bioenergy were also achieved, mainly focusing on biodiesel synthesis, and new products like biokerosene for aviation (Klein et al. 2018; Zelt 2017) and raw residual biomass feedstock for solid biofuel production (Evaristo et al. 2016a) were introduced. Publications on human health and nutrition reported on hypoglycemic (da Silva et al. 2018; Nunes et al. 2018), anti-inflammatory (Pérez et al. 2017), and nutraceutical (de Almeida et al. 2018) properties of acrocomia oil, while other studies discovered anti-cancer, anti-microbial (Souza et al. 2017a), and photoprotective (Dario et al. 2018) properties of oils. A number of post-harvesting (drying and storing conditions for oil quality maintenance) and pre-processing methods (e.g., oil extraction, enzymatic hydrolysis) were explored (Evaristo et al. 2016b; Favaro et al. 2017; Silva et al. 2017). A new study on the effects of maturity stages on kernel oil reported variations in physicochemical characteristics and composition, thus contributing to a better understanding of the ripening process (Souza et al. 2018). During this period, further studies on sustainability aspects were published, providing insights on sustainable supply of acrocomia as an alternative source of vegetable oil. The potential environmental impact of acrocomia cultivation was assessed in a life cycle analysis (Fernández-Coppel et al. 2018) and a simulation of its energy balance and greenhouse gas emissions (Evaristo et al. 2018). In 2018, the first publication on acrocomia's social sustainability was published. It evaluated aviation biofuel from a supply chain perspective, assessing employment, working conditions, labor rights, gender equity, and social development (Wang et al. 2018).

From 2019 until mid-2020, 69 articles were published. Approximately half of these investigated products and applications of acrocomia oils and leaf and fruit components, illustrating a range of processing strategies. Reported uses include briquettes as energy carriers (Costa et al. 2019), biochar (Guilhen et al. 2019; Rodriguez Correa et al. 2019), activated carbon (Barbosa et al. 2020; Moreira et al. 2020a), composite material for brick production (Calvani et al. 2020), cellulose nanocrystals from leaf fibers (Corrêa et al. 2019), plasticizers from oil (Alarcon et al. 2020), and biofilms based on pulp flour and fruit residues as substrate for enzyme production (da Silva et al. 2020a; Lopes et al. 2020). A phytochemical study of *A. totai* leaves revealed a new chemical compound that inhibits cell growth, called "totaiol," potentially allowing for medicinal applications (Souza et al. 2019a). Leaf extracts were found to exhibit antioxidant properties with low toxicity (Monteiro-Alfredo et al. 2020). Da Silva et al. (2018) and Nunes et al. (2018) reported that kernel and pulp oils show hypoglycemic effects. Bioactive and sensorial properties of fruits have also been investigated with respect to the nutritional aspects of direct consumption, a traditional activity in Chaco regions (Bortolotto et al. 2019; Teixeira et al. 2019). Nutraceutical studies have explored the use of acrocomia fruits as a complement to high-protein diets and the bioaccessibility of essential minerals contained in the pulp, identifying it as a potential source of Cu, Fe, Mn, and Zn with a high nutritional value (Almeida et al. 2020; Gonçalves et al. 2020). Furthermore, lipid extracts from *A. crispa* fruits were shown to have properties protecting against lung and kidney diseases in mice (Mena et al. 2019; Oyarzábal-Yera et al. 2019). The use of kernel and pulp cakes as animal feed is still under exploration, e.g., with regard to rumen degradability in sheep and inclusion of pulp cake in the diets of broilers and rabbits (Ferreira et al. 2019a, 2019b; Neta et al. 2019).

Current research continues to investigate the physicochemical characteristics of oil and effects of ripening, harvest time, and post-harvest practices on oil quality. A study on the maturity process of acrocomia fruits concluded that fatty acid and triacylglycerols proportions of both pulp and kernel oils remain constant during the ripening process, but the oil content of the mesocarp increases at the end of the maturation period (Lieb et al. 2019). This study sheds light on harvesting practices, recommending that bunches are harvested at an advanced stage of maturity. A complementary study on the effects of storage period lengths on mesocarp quality parameters concludes that non-pre-treated, fully ripe fruits harvested directly from the bunch can be stored at room conditions for up to 20 days with oil quality remaining within desired limits (Tilahun et al. 2019). With the aim of extending this period and avoiding deterioration of the mesocarp, a number of post-harvest methods were explored including the use of ozone gas on fresh fruits, irradiation, and air drying (da Silva et al. 2020b; Silva et al. 2019a, 2019b; Tilahun et al. 2020). Other studies investigated the applicability of new biocatalysts for hydrolyzing high-acid mesocarp oil (Rade et al. 2020) and emerging oil extraction methods (da Rosa et al. 2019b). The effect of the mechanical pressing temperature on the quality and composition of mesocarp oil was investigated for the first time. It was found that oil quality and stability were higher under cold pressing conditions and appropriate harvesting and post-harvesting practices (Prates-Valério et al. 2019). Thermal behavior of acrocomia oils and biodiesel from kernel oil has also been investigated, providing important kinetic data on thermal effects on nutritional properties and phase transitions for further industrial applications (de Moura et al. 2019; Magalhães et al. 2020; Menezes et al. 2019).

Successive fundamental and applied research on plant science and agronomy embrace studies on ecophysiology, plant germination, plant breeding, and crop management. Studies on the influence of atmospheric CO_2 on the response of acrocomia to drought and soil physicochemical attributes contributed to the understanding of non-biotic factors affecting the plant (Rosa et al. 2019b). These included the impact of climatic and edaphic factors on the germination process of *A. aculeata* in soil seed banks (Souza et al. 2019b). Environmental factors (i.e., precipitation and relative humidity) coupled with genetic variability may also influence biometric parameters, oil content, and composition of *A. aculeata* fruits, as has been shown by the analysis of populations at different locations in Costa Rica (Alfaro-Solís et al. 2020). It was also found that small-sized fruits had a higher mesocarp oil content, indicating potential targets for selection (Alfaro-Solís et al. 2020). Genetic studies included a gene flow analysis to estimate the effective population size of *A. aculeata* in Brazil's Atlantic Forest (Portela et al. 2020), the characterization of fruit accessions, and the estimation of genetic parameters for the selection of progenies with specific targets such as productivity, adaptability, and stability (dos Reis et al. 2019; Rosado et al. 2019). In the field of plant propagation, somatic embryogenesis from leaf tissues has recently been introduced, contributing to the understanding of the embryogenesis process (Meira et al. 2019). Other publication adding relevant information for crop management includes an evaluation of acrocomia's root system (Moreira et al. 2019), studies of potential pests, e.g., *Raoiella indica* and *Cyclocephala forsteri* (Maia et al. 2020; Souza et al. 2020), a model to estimate bunches weight (Malaquias et al. 2019), and the validation of a prototype for harvesting by mechanical vibration (Grupioni et al. 2020). Carbon sequestration in cultivated acrocomia and potential carbon credit generation were assessed for the first time (Moreira et al. 2020b). Socio-economic effects and human health impacts of acrocomia-based aviation biofuels contributed to the social dimension of sustainability studies (Wang et al. 2019, 2020).

3.3 Trends in and drivers of acrocomia research

Acrocomia research has diversified considerably during the period assessed in this review, with processing and product development as dominant research areas (Fig. 3). Since 2001, a range of bioenergy products (both solid and liquid energy carriers) and their corresponding pathways have been developed. These include biodiesel, bioethanol, aviation biofuels, bio-oil, straight vegetable oil, charcoal, and raw residual biomass. Up till 2018, biodiesel, including aviation biofuel, accounted for 73.6% of total bioenergy research, with most publications, specifically in biodiesel research, originating from Brazil. This can be explained by the energy policies put into practice by Brazil's government to support biodiesel production and reduce dependence on petroleum (César and Batalha 2010), e.g., a mandatory diesel blend (10% biodiesel). Additionally, the National Program for the Production and Use of Biodiesel (PNPB), launched in 2004 by the Ministry of Science and Technology of Brazil, introduced mechanisms and policies to foster the inclusion of smallholder farmers in biodiesel production in less developed regions. However, such mechanisms have proved insufficient to effectively increase the participation of family farmers in the bioenergy sector (César and Batalha 2010).

After bioenergy, the second largest increase in research publications can be seen for the area of health and nutrition. This indicates a rise in interest in bioprospecting aimed at the discovery of new natural products such as nutraceuticals, bioactive compounds, and medicinal applications. Of all publications allocated to the area of processing and products, 24.3% relate to the characterization of bioactive compounds, nutritional analysis, properties, and applications of oils and identification of traditional uses of acrocomia-based products in the food and health sectors. These include the nutritional analysis of carotenoids and tocopherols, primarily from pulp and kernel oils but also from roots and leaves. Research on processing and products also covers a wide range of biomaterials for various industrial sectors and conversion pathways to valorize residual biomass from oil extraction (e.g., husk, endocarp, and press cakes) into animal feed, platform chemicals, adsorbents, substrates for enzyme production and biocomposites, among others (Caldeira et al. 2018; Carrera et al. 2012; Lacerda et al. 2015; Souza et al. 2015). This illustrates the potential of designing biorefinery concepts as a strategy for the integral processing of acrocomia into a diverse spectrum of material and energetic products.

Given acrocomia's potential as a multipurpose crop, its domestication should be integral and systematic. Its cultivation and deployment depend on progress in breeding, genetics, and agronomics. Although the number of publications on biomass production and fundamental research on plant science was found to be lower than for processing and products, the last decade saw a significant increase. At fundamental level, these publications are related to botany, specifically taxonomy, genetics, ecophysiology, and plant reproduction, addressing questions of phenotypic plasticity to environmental factors, genetic variability, taxonomic classification, as well as reproduction mechanisms, flowering, and fruit development. At applied level, research on propagation has contributed significantly to domestication, possibly associated with the 2007 patent on pre-germination of *A. aculeata* seeds (Motoike et al. 2007). The main research propagation topics include seed dormancy and treatments to stimulate germination, embryo development, and viability. Additionally, somatic embryogenesis emerged in the last decade as a promising propagation alternative for acrocomia. The following section explores the progress toward complete domestication for understanding the state-of-the-art and identifying gaps with respect to acrocomia's preparedness for cultivation.

Increasing attention to sustainability aspects has recently been observed, as can be seen in the growing number of *ex ante* studies on environmental and social impacts associated with acrocomia cultivation, production of aviation biofuel, and use of by-products as animal fodder. Integrated agricultural systems (i.e., agroforestry) and use of degraded lands are highlighted as potential strategies for its sustainable cultivation.

3.4 Acrocomia's preparedness for cultivation

Despite the socio-economic importance of acrocomia in countries like Paraguay and Brazil and the potential for the establishment of acrocomia-based value webs, this palm has not yet been fully domesticated. Its traditional and industrial uses rely on wild harvesting as the initial step in the multi-staged domestication process (Kantar et al. 2017). However, significant progress toward crop development and cultivation has been reported in the scientific literature in both fundamental and applied research. In the following sections, the acrocomia's preparedness for cultivation will be assessed by reviewing the findings from fundamental to applied research along the crop development process. This encompasses genetic and phenotypic levels, pre-breeding steps, breeding, germination and propagation, and crop management and cultivation systems.

3.4.1 Genetic and phenotypic diversity

3.4.1.1 Plant taxonomy *Acrocomia* spp. display high phenotypic diversity and a complete taxonomic classification of the genus has yet not been reported (de Lima et al. 2018). So far, seven caulescent species have been preliminary identified: *A. aculeata*, *A. totai*, *A. intumescens*, *A. media*, *A. crispa*, *A. corumbaensis*, and *A. glaucescens*. The latter is described as a dwarf species, whereas the others are of tree size (Vianna et al. 2017b). Two acaulescent species are also described: *A. hassleri* and *A. emensis* (Vianna et al. 2017b). A number of these apparent species have been also considered synonyms (e.g., *A. sclerocarpa*), indicating the uncertainty surrounding the classification of the genus (de Lima et al. 2018; Lanes et al. 2015). A detailed comparison of morphological traits of *Acrocomia* spp. is presented in the taxonomy review by de Lima et al., (2018). The authors conclude that, based on morphological traits and habitat, *A. totai* and *A. intumescens* are two distinct species (de Lima et al. 2018). Additionally, phylogenetic relationships suggest that the latter and *A. aculeata* are distinct species, although there is a lack of integral evidence from phylogenetic studies (de Lima et al. 2018). Other studies reviewed by de Lima et al. (2018) reported the possible occurrence of ecotypes (Machado et al. 2015; Pires et al. 2013) and the hypothetical ongoing specialization and speciation of the genus (Lanes et al. 2015). Some studies observed different genetic clusters among populations of *A. aculeata* and *A. totai* and morpho-anatomic differences between multiple *Acrocomia* spp. (Abreu et al. 2012; Lanes et al. 2015; Vianna et al. 2017b). Variation in fruit biometry and in morphological characteristics, such as stem appearance among *A. aculeata*, *A. intumescens*, and *A. totai*, provides confirmation that they are distinct species (Vianna et al. 2017a). Phylogenomic analyses using the complete plastome of *A. aculeata* and plastomes of 40 taxa from all five subfamilies of Arecaceae indicate *A. aculeata* as an Arecoideae species that belong to the tribe Cocoseae, close to the genus *Elaeis* (Lopes et al. 2018). Beyond these achievements, a comprehensive understanding of *Acrocomia* spp. and their distribution is required for plant domestication and formulation of conservation strategies for native populations (de Lima et al. 2018; Gauto et al., 2011; Vianna et al. 2017b), providing an entry point for breeding and crop improvement. In this way uncertainty could be reduced, allowing a clear discrimination of species in research activities, as today manifold publications consider acrocomia as *A. aculeata* without full knowledge on the genus taxonomy (de Lima et al. 2018).

3.4.1.2 Genetic diversity The genetic diversity of *A. aculeata* within determined geographical locations has so far mainly been studied in Brazil. Lanes et al. (2015) identified the state of Minas Gerais (Brazil) as the center of *A. aculeata*'s genetic diversity, based on detected gene pools and population parameters such as allele richness number, polymorphism, and heterozygosity within and between populations. Various genetic studies conclude that *A. aculeata* presents high polymorphism, which indicates high genetic diversity (Table 2). The average number of alleles per locus in all populations of adult plants studied in diverse regions of Brazil ranges from 3.28 to 9.4. In these studies, average observed heterozygosity has values between 'zero' and 'one,' whereas expected heterozygosity ranges from 'zero' to 0.828. A high positive fixation index and low heterozygosity in juvenile plants in comparison to adult individuals suggest recurrence of inbreeding and selection against homozygotes throughout developmental stages (Araújo et al. 2017; Lanes et al. 2016). Thus, genetic diversity apparently reduces over generations through inbreeding (Araújo et al. 2017). Limited gene flow between isolated populations—but also between populations in close proximity—leads to inbreeding, formation of genetic structures, and genetic differentiation. This limitation is caused by a spatially constrained dispersion of

Table 2 Genetic diversity parameters of natural populations of acrocomia. Average values of all populations included in each study; k = number of alleles per locus; H_o = observed heterozygosity; H_e = expected heterozygosity; F = fixation index.

Palm species	k	H_o	H_e	F	Location in Brazil	Sample size	References
A. aculeata	6.2	0.483	0.57	0.148	Pontal do Paranapanema and municipality of Amparo, São Paulo state	200 individuals/4 populations	Coelho et al. (2018)
A. aculeata	9	0.37	0.787	-	States of São Paulo, Minas Gerais, Mato Grosso do Sul, Pará, Pernambuco, Paraiba	77 accessions	Lanes et al. (2015)
A. aculeata	5.3	0.527	0.678	0.219	South-eastern Brazil, state of Minas Gerais	27 adult individuals	Lanes et al. (2016)
	6.1	0.441	0.700	0.433		157 juvenile individuals	
A. aculeata	4.2	-	0.399	-	Northern Minas Gerais	10 individuals/5 populations	Oliveira et al. (2012)
A. aculeata	3.28	0 – 1.0	0 – 0.828	-	States of São Paulo and Minas Gerais	17 individuals	Bazzo et al. (2018)
A. aculeata	7.2	0.37	0.54	0.33	States of São Paulo, Minas Gerais, Mato Grosso do Sul, Pará, Pernambuco, Paraiba	192 accessions	Mengistu et al (2016b)
A. aculeata	9.4	0.516	0.733	0.296	State of Minas Gerais	72 adult individuals	Araújo et al. (2017)
	10.4	0.575	0.68	0.155		144 juvenile individuals	
	10.5	0.398	0.651	0.388		600 progenies	
A. emensis	9.94	0.148	0.695	0.789	North of Minas Gerais	150 individuals/3 populations	Neiva et al. (2016)

Table 3 Available molecular biology resources for acrocomia. [a]Three additional SSR markers were proposed by (Nucci 2007) as indicated by (Mengistu et al. 2016b).

Species	Molecular biology resources	Description	References
A. aculeata	145 EST-SSR markers	Transcriptome analysis of eight tissues (leaves, leaf sheaths, roots, bulbs, fruit, male, and female flowers from native plants located in São Paulo (Brazil)	Bazzo et al. (2018)
A. aculeata	8 SSR markers[a]	Polymorphic markers from leaf tissue, four different populations in São Paulo and Minas Gerais (Brazil)	Nucci et al. (2008)
A. aculeata	221 SSR markers	Complete plastome from leaf tissue from Macaúba Active Germplasm Bank (BAG-Macaúba)	Lopes et al. (2018)

pollen and seeds and probably also by asynchronous flowering (Abreu et al. 2012; Coelho et al. 2018; Lanes et al. 2015; Portela et al. 2020). However, synchronized fertilization throughout the inflorescence was observed in *A. aculeata*, evidencing no relation with irregular fruit abscission (Mazzottini-dos-Santos et al. 2015a). An analysis of gene flow and migration indicated that geographically proximal populations have high migration rates, which influence mutation and variability in populations, possibly increasing their genetic homogeneity (Portela et al. 2020). The authors found that, in a population of *A. aculeata* located in a fragmented area distant from other populations, extinction of local genotypes may occur through geographical and ecological barriers restricting gene flow (Portela et al. 2020). Populations with high probability of inbreeding in fragmented areas exhibit presence of private alleles, an indication of genetic differentiation (Coelho et al. 2018; Nucci et al. 2008). Evidence of high genetic diversity, clustering, and structuring of groups based on various traits, mainly morphological, has also been found for *A. aculeata* in various regions of Brazil (Coser et al. 2016; da Conceição et al. 2015; Domiciano et al. 2015; dos Reis et al. 2017, 2019; Manfio et al. 2011). In the case of *A. emensis*, genetic diversity parameters indicate an excess of homozygotes, thus high occurrence of inbreeding (Neiva et al. 2016). These findings underline the importance of outcrossing genotypes from distant areas as a strategy for introducing heterosis effects, thus contributing to crop development and acrocomia's preparedness, particularly *A. aculeata.*

3.4.1.3 Available molecular biology resources Sequencing data from *A. aculeata* have been increasingly generated from 2008 onward. This provides useful genomic tools for species conservation and pre-breeding, allowing the assessment of natural populations, characterization of genetic diversity, and analysis of germplasm. Initial genomic libraries were established by Nucci et al. (2008), who identified eight polymorphic SSR markers from *A. aculeata* (Table 3). Bazzo et al. (2018) reported the identification of 418 EST-SSR markers from different *A. aculeata* tissues by transcriptome sequencing and the validation of 145 of these. A high cross-species transferability level of these EST-SSR markers was

Table 4 Accessions from natural populations of *Acrocomia* spp. characterized in genetic studies.

Collection (from natural populations)	Geographical coverage	Type of study	References
Germplasm bank BAG–Macaúba: 302 accessions, 253 maternal families	Almost all regions of Brazil	Diverse purposes	Coser et al. (2016; Lanes et al. (2016); Pires et al. (2013)
Experimental unit Santa Elisa – IAC	São Paulo state, Brazil	Diverse purposes	Bazzo et al. (2018)
93 individuals in 10 locations	São Paulo state, Brazil	Genetic structure and mating system	Abreu et al. (2012)
200 individuals, 4 populations	São Paulo state, Brazil	Genetic diversity, genetic structure, and mating system	Coelho et al. (2018)
10 individuals, 49 genotypes, 5 sites (natural populations)	Northern Minas Gerais, Brazil	Genetic diversity	Oliveira et al. (2012)
70 plants, 3 natural population	Mato Grosso do Sul, Brazil	Phenotypical characterization	Vianna et al. (2013)
35 genotypes	States of Minas Gerais, Goiás, Tocantins, Distrito Federal, Brazil	Genetic diversity	da Conceição et al. (2015)
27 individuals	State of Minas Gerais, Brazil	Genetic structure and mating system	Lanes et al. (2016)
130 accessions from 35 municipalities	Goiás state, Brazil	Genetic diversity	dos Reis et al. (2017)
145 samples	States of Minas Gerais, São Paulo, Mato Grosso do Sul, Pará, Maranhão, and Pernambuco, Brazil	Biometric characteristics	Manfio et al. (2011)
15 families	States of Minas Gerais, Goiás, and Distrito Federal, Brazil	Genetic variability and genetic parameters	Domiciano et al. (2015)
137 accessions	Goiás state, Brazil	Biometric characteristics	dos Reis et al. (2019)
43 individuals	States of Minas Gerais and São Paulo, Brazil	Genetic diversity	Nucci et al. (2008)
816 individuals	State of Minas Gerais, Brazil	Genetic structure and gene flow analysis	Araújo et al. (2017)
200 individuals, 4 populations	São Paulo state, Brazil	Gene flow and effective population size	Portela et al. (2020)

detected, with rates above 98% for *A. totai* and *A. intumescens* and values ranging from 71.7% to 80.7% for other palm species (Bazzo et al. 2018). Cross-species transferability of SSR markers sourced from other Arecaceae taxons has been examined by Mengistu et al. (2016b), resulting in the identification of seven markers transferable to *A. aculeata*. The complete plastome of *A. aculeata* was reported by Lopes et al. (2018), resulting in the identification of 113 unique genes and 221 SSR loci. The availability of a larger collection of molecular markers is necessary to enable genetic analysis and germplasm management of acrocomia and also breeding and genomic selection strategies.

3.4.1.4 Germplasm collections In 2009, an acrocomia germplasm bank (BAG–Macaúba) was established by the Federal University of Viçosa in Araponga, Minas Gerais, Brazil. It is an ex situ collection of *A. aculeata* that contains 302 accessions (open-pollinated progenies) and a total of 253 maternal families from almost all regions of Brazil. BAG–Macauba is one of the largest collections of *A. aculeata* germplasm in South America registered by the Brazilian Board of Genetic Heritage (# 084/2013-SECEX/CEGEN). The plants added to the germplasm bank originated from seeds collected from natural populations and were pre-germinated following the protocol patented by Motoike et al. (2007) (Coser et al. 2016; Lanes et al. 2016; Pires et al. 2013). A collection of *A. aculeata* adult plants at the experimental unit Santa Elisa – IAC (Agronomic Institute of Campinas), located in Campinas (state of São Paulo, Brazil), has been used for identification of microsatellites for genetic studies (Bazzo et al. 2018). In addition to these collections, unofficial accessions mainly from native Brazilian populations of *A. aculeata* have been reported in diverse genetics studies (Table 4). In other regions of Latin America, germplasm collections are still required, including accessions of other *Acrocomia* spp., e.g., *A. totai*.

3.4.2 Adaptability to the environment and phenotypic plasticity

Acrocomia presents phenotypic plasticity allowing palms to adapt to a wide variety of ecoregions and environments under different climate and soil conditions (Coelho et al. 2017; Lanes et al. 2015). This underlines the importance of understanding interactions between genotypes and environment (Rosado et al. 2019). Large plasticity in botanical components of *A. aculeata* was observed in a study in the state of São Paulo (Brazil), possibly caused by environmental factors including soil fertility and soil water availability, in turn influenced by particle size distribution, soil drainage, and climate. These factors contribute to the stratification of the species (Coelho et al. 2017). Biometric traits of *A. aculeata*, such as fruit mass, fruit size, number of productive bunches, and stem circumference, correlated with non-biotic factors like soil drainage (Coelho et al. 2017). According to the authors, fruit mass and size were the variables that correlated most with soil fertility and soil particle size. In contrast, plant height, number of bunches per palm, and quantity of productive bunches do not correlate with these environmental factors and can be explained by plant age, genetics, phenology, or biannuality (Coelho et al. 2017). Among the determinants of pulp oil content, high precipitation probably has a strong influence (Alfaro-Solís et al. 2020). In addition, mild temperature (20.7 °C) is associated with higher values of measurable characteristics of *A. aculeata* fruits (Castro et al. 2017).

Evidence of *A. aculeata*'s distribution in three regions of Minas Gerais (Brazil) reveals that this plant adapts better to areas with more fertile soils and with forest, particularly semi-deciduous forest, as primary vegetation (Coelho et al. 2017; da Motta et al. 2002). Interestingly, *A. aculeata* adapts to soils with varying acidity profiles and its occurrence is limited in areas with low drainage (Coelho et al. 2017). A number of plant traits were found to be influenced by pedogenesis. Higher values of fruit size, fruit mass, and plant height were found for soils developed from granitic rocks and higher number of productive bunches for soils derived from basic rocks (Coelho et al. 2017). Moreover, the phosphorus content of soil was associated with *A. aculeata* seed input, leading to the formation of persistent soil seed banks (Souza et al. 2019b). Other edaphic factors were found to be detrimental (i.e., sand, organic matter, and clay content) for seed survival and germination (Souza et al. 2019b). *A. aculeata* has the ability to maintain viable, dormant seeds with rich endospermic resources in the soil for long periods, enabling its reproductive capacity, wide distribution, and adaptation to different environments (Mazzottini-dos-Santos et al. 2017; Souza et al. 2019b).

Acrocomia exhibits drought tolerance, a key trait for adaptability to and productivity in marginal environments (Mota & Cano 2016; Rosa et al. 2019b). In fact, palms of this genus grow naturally under environmental conditions with seasonal droughts and high temperatures (Pires et al. 2013). *A. aculeata* is able to maximize light capture and photosynthetic response to different lighting conditions both at the nursery stage and in the field and to apply continuous adjustments throughout early-stage development (Dias et al. 2018; Pires et al. 2013). Juvenile *A. aculeata*'s plants display an increasing net photosynthetic rate during the morning hours, reaching a peak before noon, and exhibit gas exchange parameters corresponding to those of C3 species (Pires et al. 2013). Water stress reduces biomass accumulation and restricts gas exchange, the latter recovering after rehydration (Mota & Cano 2016; Oliveira et al. 2016). The efficient photosynthetic mechanisms of *A. aculeata* prevent metabolic damage from water stress, allowing a fast and complete recovery of the plant (Rosa et al. 2019b). The performance of *A. aculeata* under semi-arid abiotic stress shows that photosynthetic pigments are not significantly affected by water availability and an increase in water use efficiency indicates drought tolerance (Oliveira et al. 2016). Moreover, long-term exposure to increased CO_2 concentration levels affects its physiology and morphology (Rosa et al. 2019b). The authors conclude that high CO_2 levels lead to up-regulation of photosynthesis resulting in higher light and water use efficiency and gain in aboveground biomass (Rosa et al. 2019b). Moreover, high CO_2 concentration levels contribute to an improved response of the plant to drought stress without loss of total dry mass, possibly advantageous for climate change adaptation (Rosa et al. 2019b). Studied responses of *A. aculeata* indicate that it is suited to a variety of environments including marginal conditions. However, the influence of abiotic factors on productivity and biomass quality has only been studied to a limited extent.

3.4.2.1 Biometric characteristics of fruits Fruit mass, size, and seed volume are among the main parameters contributing to variability among accessions of *A. aculeata* in Brazil that may be affected by environmental factors (dos Reis et al. 2017). The average diameter of *A. aculeata* fruits from different regions of Brazil ranges between 2.8 and 4.7 cm, with little variation between vertical and horizontal dimensions due to the nearly spherical shape of the fruits (Ciconini et al. 2013; dos Reis et al. 2017; Sanjinez-Argandoña & Chuba 2011; Vianna et al. 2013, 2017a). *A. aculeata* fruits present a larger transversal diameter (mean = 4.1 cm) than *A. intumescens* (mean = 3.7 cm) and *A. totai* (mean = 3 cm) (Machado et al. 2015; Vianna et al. 2017a). Da Conceição et al. (2015) found the fresh fruit mass of *A. aculeata* in various regions of Brazil to range between 23.9 and 58.6 g (mean = 41.2 g). Similar figures for this species have been reported for Costa Rica (Alfaro-Solís et al. 2020). Lower fruit mass for the same species (between 12 and 23.5 g on a fresh basis) was observed in Mato Grosso do Sul (Brazil) (Ciconini et al. 2013). The lowest mass values reported for *A. aculeata* fruits oscillate between 7.8 and 11.4 g (dos Reis et al. 2017, 2019). *A. intumescens* and *A. totai*'s fruits have lower mass values than *A. aculeata*, at an average of 29 g and 16.6 g (fresh basis), respectively (Machado et al. 2015; Markley 1955; Vianna et al. 2017a). Fruits from *A. sclerocarpa*, synonym of *A. aculeata* (de Lima et al. 2018), from Minas Gerais (Brazil) are larger and heavier than *A.*

aculeata fruits, with an average width of 5 cm and mass of 66.8 g (Machado et al. 2015). Moisture values of *A. aculeata* fruits range from 31 to 63% (Alfaro-Solís et al. 2020; Ciconini et al. 2013; Vianna et al. 2017a). *A. totai*, *A. sclerocarpa*, and *A. intumescens* fruits have an average moisture of 44%, 45.9%, and 39.6%, respectively (Machado et al. 2015; Vianna et al. 2017a). Concerning the composition of *A. aculeata* fruits, the epicarp accounts for 17.9 – 32.6%, the mesocarp 41 – 51.2%, the endocarp 22 – 31%, and the kernels 4.9 – 9% (Alfaro-Solís et al. 2020; Ciconini et al. 2013; da Conceição et al. 2015; Sanjinez-Argandoña & Chuba 2011). *A. totai* fruits presented a higher mesocarp (53.3%) and lower endocarp content (20.6%), whereas *A. sclerocarpa* fruits exhibited higher epicarp (34.7%) and lower endocarp (15.7%) and kernel (3.1%) contents (Machado et al. 2015). These findings indicate a large variability in fruit size and fractions. Whether this is dominated more by genotype or environmental factors has, however, not been confirmed.

3.4.2.2 Biometric characteristics of oils Mesocarp and kernel oil content are biometric traits that contribute to divergence among *A. aculeata* genotypes, with mesocarp oil and its fatty acid profile having a greater influence (da Conceição et al. 2015; dos Reis et al. 2017). Mesocarp oil content was found to vary widely between fruits from different regions of Brazil (between 14.6 and 77.5% on a dry basis, mean = 55.7%) (da Conceição et al. 2015). Other studies have observed an oil content (on dry basis) in *A. aculeata* fruit mesocarp of around 25% in Brazil and between 23.4 and 39.6% in Costa Rica (Alfaro-Solís et al. 2020; Ciconini et al. 2013; Coimbra & Jorge 2011, 2012; Lescano et al. 2015b; Lieb et al. 2019). Values of 32%, 32.8%, and 29.6% (dry basis) have been measured for *A. totai*, *A. sclerocarpa*, and *A. intumescens* fruits, respectively (Machado et al. 2015; Silva et al. 2015). Results from a study in Costa Rica suggest that pulp oil content may be more influenced by environmental and genetic variation than kernel oil content (Alfaro-Solís et al. 2020).

Acrocomia fruit kernels have a higher oil content. For *A. aculeata* fruits from the Brazilian states of Minas Gerais, Federal District, Goiás and Tocantins, it ranges from 33.2 to 61% (dry basis, mean = 45.8%) (da Conceição et al. 2015). Higher values of 63.5 to 68.9% have been observed in Mato Grosso do Sul (Ciconini et al. 2013). In Costa Rica, the average oil content of *A. aculeata* fruit kernels has been found to range from 48.7 to 58.4% on a dry basis (Alfaro-Solís et al. 2020; Lieb et al. 2019). Kernels from *A. totai* fruits in the state of Paraná exhibited an average oil content of 58.3% in the final stages of ripening (Souza et al. 2018), higher than the value of 47.76% reported by Machado et al. (2015) for fruits from the same region and species. *A. sclerocarpa* displays a value (55.4%) similar to those of *A. aculeata* and *A. totai* (Machado et al. 2015).

Mesocarp oil from acrocomia fruits is composed predominantly of unsaturated fatty acids (~72.5%) (Coimbra & Jorge 2012; de Oliveira et al. 2017; del Río et al. 2016; Lescano et al. 2015b; Lieb et al. 2019; Silva et al. 2015), with the main fatty acids present being oleic and palmitic acid. Palmitoleic, vaccenic, linoleic, and stearic acid are found in minor proportions (del Río et al. 2016; Lieb et al. 2019). There is wide variation in fatty acid profiles of fruits from natural palms located in different areas (Fig. 4). Oleic and palmitic acid play a large role in the differentiation of genotypes of *A. aculeata* in Brazil (da Conceição et al. 2015).

By comparison, kernel oil from acrocomia fruits has a high composition of saturated fatty acids (~71%) (Coimbra & Jorge 2012; de Oliveira et al. 2017; del Río et al. 2016; Lescano et al. 2015b; Lieb et al. 2019; Silva et al. 2015; Souza et al. 2018), from which lauric, oleic, and myristic acid are the main fatty acids. Palmitic, caprylic, capric, stearic, and linoleic acid are found in minor proportions. Lauric and oleic acids make a major contribution to genetic variation in kernel oil fatty acid contents of *A. aculeata* in Brazil (da Conceição et al. 2015).

3.4.2.3 Fruit and oil productivity A few studies address the predictive productivity modeling of acrocomia and the correlation of physical variables, among them Castro et al. (2017), Ciconini et al. (2013), and Malaquias et al. (2019). The number of bunches per *A. aculeata* palm in the Cerrado and Pantanal regions of Brazil varied from two to five, presenting high variability, with number of fruits ranging between 320 and 1080 per palm, resulting in 13.7 to 25.5 kg of fruits per palm (Ciconini et al. 2013). Assuming an average weight of 24.5 kg per fresh bunch and a mean number of 2.36 bunches per *A. aculeata* palm, a single palm older than ten years could produce up to 57.8 kg, of which the empty bunch contributes 1 kg (Evaristo et al. 2018). Potential increases may be achieved with a greater number of bunches (Evaristo et al. 2018). Other studies report an average of seven bunches per palm, with up to 15 bunches in the states of Mato Grosso do Sul and Minas Gerais (Malaquias et al. 2019; Sanjinez-Argandoña & Chuba 2011). Observations for *A. totai* indicate between three and eight bunches per palm (Markley 1955). There is high degree of uncertainty with respect to the age of the palms included in these studies, which are mainly based on native populations.

Ciconini et al. (2013) found the total mass of fruits to be associated with their number and that an increase in number does not reduce the mass of individual fruits. This suggests that a high yield may be associated with the number of fruits per bunch, which could be a criterion for selection. The authors observed that fruit mass shows a strong correlation with epicarp and mesocarp mass and, to a lesser extent, with kernel and endocarp mass (Ciconini et al. 2013). There is little correlation between biometric fruit characteristics and

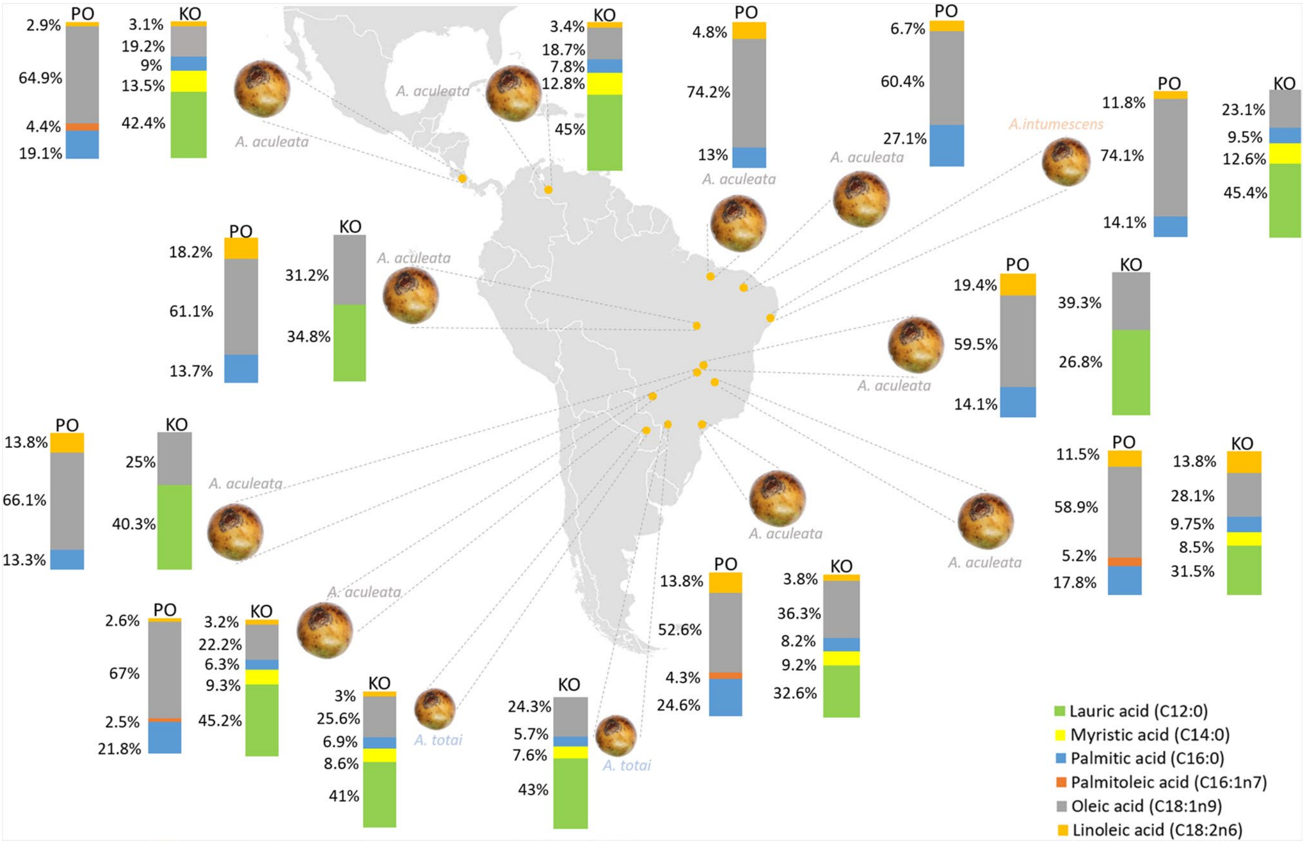

Fig. 4 Main fatty acids in pulp or mesocarp oil (PO) and kernel oil (KO) from *Acrocomia* spp. in various regions of Latin America. Average data from Alfaro-Solís et al., 2020; Coimbra & Jorge, 2012; da Conceição et al., 2015; de Oliveira et al., 2017; del Río et al., 2016; Favaro et al., 2017; Hernández et al., 2007; Ribeiro et al., 2017; Lescano et al., 2015b; Lieb et al., 2019; Navarro-Díaz et al., 2014; Silva et al., 2016; Silva et al., 2015; Souri, 2017; Souza et al., 2018; Trentini et al., 2017.

oil content. Observations from Costa Rica and the Pantanal Region of Brazil indicate an inverse relationship between fruit size and oil concentration (Alfaro-Solís et al. 2020; Ciconini et al. 2013). Mesocarp oil content exhibits a strong positive correlation with total fruit oil, but a negative correlation with the mesocarp's proportion of the whole fruit (Ciconini et al. 2013; da Conceição et al. 2015). Costa et al. (2018b) observed a low correlation between oil content and oil yield per plant, which indicates that the latter depends more on the number of fruits per plant than on oil content of the individual fruits. Further information is needed on selection criteria such as fruit yield, oil concentrations, and corresponding correlations to assist the breeding of commercial varieties of acrocomia.

3.4.3 Pre-breeding

3.4.3.1 Reproductive biology *A. aculeata* is a monoecious species (both male and female flowers are present in the same inflorescence) with marked protogyny, which flowers from October to December (Scariot et al. 1991; Mazzottini-dos-Santos et al. 2015a). Flowers present high genetic and biometric variability and phenotypic plasticity (Mazzottini-dos-Santos et al. 2015a). The authors characterized the floral biometry, morphology, and anatomy in *A. aculeata*. This plant has a mixed mating system with predominance of outcrossing (allogamous mating system) with beetles, small bees, and wind as pollination vectors (Abreu et al. 2012; Coelho et al. 2018; Henderson et al. 1995; Lanes et al. 2016; Scariot et al. 1995). Seeds are dispersed primarily by barochory and secondarily by dispersal agents including large mammals (e.g., primates, marsupials, tapirs, and capybaras), birds (e.g., macaws and rheas), water, and wind (Araújo et al. 2017; Coelho et al. 2018; Lanes et al. 2015, 2016). *A. aculeata* exhibits inbreeding preference and individual variation of self-incompatibility based on low levels of selfing in isolated or fragmented habitats (Abreu et al. 2012; Araújo et al. 2017; Coelho et al. 2018; Lanes et al. 2016; Scariot et al. 1995). A low correlation paternity was observed in one population of *A. aculeata* in São Paulo state, indicating a high probability of half-sib occurrence (Coelho et al. 2018), random mating, and uncommon mating between related individuals. The authors found an absence of intrapopulation spatial genetic structure. On the contrary, progenies from the same species in Brazil's south-eastern region present a high paternity correlation suggesting biparental inbreeding (same parental and maternal plant) and a high probability of full-sibs, possibly due to intrapopulation spatial genetic structures (Araújo et al. 2017; Lanes et al. 2016). This indicates that outcrossing may not be a random event. A high inbreeding or endogamy coefficient was also observed for populations of *A. emensis* in Minas Gerais (Neiva et al. 2016). Lanes et al. (2016) point out that assuming progenies as half-sibs would imply overestimation of diverse factors such as additive genetic variance, heritability, and genetic gains from selection. The authors estimate that, for the areas under study, the maintenance of an effective population size for conservation and seed collection programs would require at least 77 under ex situ and 258 individuals under in situ conditions (Lanes et al. 2016). In contrast, the estimated number of palms for seed collection in a population located in the state of São Paulo exhibiting low inbreeding is 40 (Coelho et al. 2018). To date, no detailed studies on the reproductive biology of other species of the genus *Acrocomia* have been reported, other than one study on *A. emensis* (Neiva et al. 2016).

3.4.3.2 Fruit development The development of *A. aculeata* fruits is slow and can last up to 62 weeks after anthesis, equivalent to 14.3 months (Mazzottini-dos-Santos et al. 2015b; Montoya et al. 2016). After a predominant size gain during the first eight weeks, fruits reach their maximum size, the greater part of their total mass and their final globose shape by week 15 (Mazzottini-dos-Santos et al. 2015b; Montoya et al. 2016). Dry mass accumulation occurs intensively between the 4th and 16th week and extends until the end of the development period (Mazzottini-dos-Santos et al. 2015b; Montoya et al. 2016). During the ripening period, the epicarp changes color from light green to bright brown, evidencing lignification within 20 days of anthesis (Reis et al. 2012). The pericarp layers (epicarp, mesocarp, and endocarp) differentiate in the initial days and reach their final thickness by week 15 to 16 (Montoya et al. 2016; Reis et al. 2012). The epicarp is the first structure to reach full growth, regulating final fruit size (Montoya et al. 2016). Accumulation of water in the fruit occurs during the first 12 weeks and decreases gradually from then onward (Mazzottini-dos-Santos et al. 2015b; Montoya et al. 2016). Dry mass accumulation of epicarp and endocarp extends until week 16 and 24, respectively, when their esclerification restricts further fruit expansion (Mazzottini-dos-Santos et al. 2015b; Montoya et al. 2016; Reis et al. 2012). Mesocarp dry mass mainly increases between the 4th and 10th week and again between the 35th and 54th week (Mazzottini-dos-Santos et al. 2015b; Montoya et al. 2016). Its color changes from cream to green and finally to yellow by week 46 when maturation is reached, with embryo and seed fully developed (Montoya et al. 2016). Endocarp expansions starts by the third week and the arrangement of sclereids in different directions by the 10th week, leading to a hardening and darkening phase that extends until week 28 (Montoya et al. 2016; Reis et al. 2012). Endosperm/seed starts solidifying (i.e., transition from liquid to solid mass) from week 15 and its dry mass accumulates from week 24 (Montoya et al. 2016). Ripening of seed occurs over a period of 32 weeks, as determined for *A. totai* fruits in the state of Paraná (Brazil) (Souza et al. 2018).

Formation of mesocarp oil peaks near to abscission (i.e., full ripeness) and follows a linear accumulation pattern from week 36 after anthesis, reaching an oil content of 55% (dry basis) by week 62 (Mazzottini-dos-Santos et al. 2015b; Montoya et al. 2016; Reis et al. 2012). Parallel to the accumulation of mesocarp oil, starch is depleted (Montoya et al. 2016). Lieb et al. (2019) found that total lipid content in the mesocarp of *A. aculeata* fruits in Costa Rica increases during maturation from 12.1% in early maturity (unripe fruits) to 23.4% (fully ripe fruits) on a dry basis. Based on these findings, an optimal harvest time of *A. aculeata* fruits would be close to abscission, around 50–60 weeks after anthesis. Oil content in kernels of *A. aculeata* is less sensitive to kernel development, having a similar during the last value 10 weeks before abscission (Mazzottini-dos-Santos et al. 2015b). Souza et al. (2018) found the kernel oil content of *A. totai* fruits to reach its highest level (67.2% dry basis) by the middle of the ripening period. Its concentration increases from 31.1% (dry basis) at an initial ripening stage to 61.3% after 12 weeks, while moisture content sharply decreases.

3.4.4 Plant breeding, germination, and propagation

3.4.4.1 Genetic parameters for selection High genetic variability among traits of interest has been found in *A. aculeata* progenies based on estimates of genetic parameters (Berton et al. 2013; Coser et al. 2016; Domiciano et al. 2015; Rosado et al. 2019). This is to be expected due to the early stage of the domestication process (Rosado et al. 2019). High heritability values indicate a strong genetic control and a good potential for selection of high-performing *A. aculeata* genotypes (Domiciano et al. 2015; Rosado et al. 2019).

3.4.4.2 Morphological traits Results of integral analyses including other parameters such as genotypic and environmental variation corroborate the assumption that the major part of the total variation in morphological traits is determined by genetics, indicating the possibility of selecting promising palm progenies for diverse traits (Berton et al.

2013; Coser et al. 2016; Domiciano et al. 2015; Rosado et al. 2019). High progeny mean heritability values have been reported for various morphological traits in *A. aculeata*, including plant height (50.2–64.5%), stem diameter (66.4%), canopy projection in the row and between rows (63.2% and 61.2%, respectively), fruit yield (67.4%), rachis length and width (71.9% and 68.2%, respectively), number of rachis (65.6%), and its total area (50.6%) (Domiciano et al. 2015; Rosado et al. 2019). Other studies included the assessment of traits, such as seed mass, and leaf and spine number (Berton et al. 2013).

Genetic parameters of fruit yield—considered as the most important trait in acrocomia breeding—indicate that this trait is favorable for selection due to its genetic control (Rosado et al. 2019). In addition to high productivity, low height is desirable to facilitate harvesting (Rosado et al. 2019). Domiciano et al. (2015) point out that, assuming photosynthesis does not contribute significantly to the differentiation of *A. aculeata* progenies, incremental productivity gains depend on morphological rather than physiological improvements. Genetic parameters of specific traits of *A. aculeata* such as epicarp, pulp, endocarp, and kernel dry matter, as well as oil content and oil yield per plant indicate considerable genetic control (Costa et al. 2018b). This was observed for oil yield in particular, the individual genetic variation of which suggests a high potential for selection and genetic gain (Costa et al. 2018b). Additional morphological traits with moderate to high heritability values at the progeny mean level include total spathe (55%), height of first spathe (72%), diameter at breast height (77%), and canopy area (46%) (Coser et al. 2016). The latter contributed the most to total variation in genotypes of *A. aculeata* from the state of Minas Gerais (Brazil).

3.4.4.3 Physiological traits Non-significant genetic variability was found for physiological traits of *A. aculeata* progenies excluding water use efficiency (Domiciano et al. 2015). This trait contributes to genetic variability and has a moderately high heritability (50.8%), thus of particular interest for selection of genotypes tolerant to water stress (Domiciano et al. 2015). Variation in germination traits across populations was evidenced for progenies of *A. aculeata*, increasing its adaptability to different environments (Berton et al. 2013). An integral analysis of genetic parameters reveals that germination rate and speed index are traits that respond well to selection due to genetics predominating over environment (Berton et al. 2013). Precocity was studied for *A. aculeata* accessions and found to exhibit a heritability at progeny mean level of 44% (Coser et al. 2016).

Genetic parameters related to genotypic stability and adaptability have also been investigated and applied for the selection of promising genotypes. Simultaneous selection for stability, adaptability, and fruit yield has resulted in genotype ordering of *A. aculeata* palms with superior performance (Rosado et al. 2019). Additional classifications for the selection of genotypes considering multiple traits have also been reported (Coser et al. 2016; Costa et al. 2018b).

3.4.4.4 Correlations between traits Correlations between traits indicate the possibility of performing indirect selection for plant breeding purposes if there is repeatability over time, a key aspect for perennial plants (Costa et al. 2018b; Domiciano et al. 2015). High repeatability coefficients for various fruit characteristics have been estimated by Costa et al. (2018b) and Manfio et al. (2011). Correlations depend on genotypic, phenotypic, and/or environmental associations in the variability of morphological and physiological traits (Berton et al. 2013; Domiciano et al. 2015). The following morphological traits stand out due to a moderately high correlation: plant height with seed mass (positive genotypic correlation); plant height with stem diameter, number of leaves, and number of spines (positive genotypic and phenotypic correlation); number of leaves with number of spines (positive genotypic and phenotypic correlation); stem diameter with number of spines (positive genotypic and phenotypic correlation); plant height with rachis length and total area; and rachis length with width and total area (Berton et al. 2013; Domiciano et al. 2015). Highest positive genotypic correlations between fruit traits were found for dry matter from endocarp and epicarp, endocarp and kernel, and pulp and oil yield per plant (Costa et al. 2018b). Stem diameter at breast height, an easily measurable trait, correlates negatively with the height of the first spathe, but positively with canopy area (Coser et al. 2016).

Observations indicate an absence of relationship between physiological and morphological traits, as well as a non-significant correlation between plant height and photosynthetic capacity (Domiciano et al. 2015). This suggests that smaller plants may exhibit a more efficient CO_2 fixation process (Domiciano et al. 2015). Progenies with a high rate of germination speed exhibit a low height and increased stem diameter, which is favorable for productivity (Berton et al. 2013). Further comparative yield studies of high- and low-height palms could shed more light on selection parameters (Domiciano et al. 2015). Berton et al. (2013) found a high positive genotypic correlation between germination rate and germination speed index. They argue that it is essential to consider these traits in the selection of plants with positive response to pre-germination methods. Additional physiological correlations were found for traits such as stomatal conductance, the relationship between mesophilic and environmental CO_2 concentration, vapor-pressure deficit, transpiration rate, and water use efficiency (Domiciano et al. 2015). Coser et al. (2016) found that accessions that are more precocious may present a larger number of spathes.

According to Costa et al. (2018b), genetic gains for oil yield per plant are estimated at 61% when superior individuals are selected. Likewise, high relative genetic gains are reported in selected plants for seed germination rate (44.9%), germination speed index (64.1%), number of spines (82.3%), plant height (53.3%), seed mass (48.2%), and stem diameter (47.5%). From an agronomic perspective, germination rate, germination speed index, seed mass, and oil yield are the most relevant for selection.

3.4.4.5 Seed germination Under natural conditions, *A. aculeata* seeds germinate slowly, reaching a cumulative germination rate of 10% between 16 and 20 weeks after sowing (Bicalho et al. 2015; Ribeiro et al. 2011; Rodrigues-Junior et al. 2016). The species naturally forms persistent soil seed banks of viable but dormant seeds whose germination (i.e., dormancy breaking) is controlled by seasonal climate variations (Ribeiro et al. 2012a; Souza et al. 2019b). Various indicators of germination potential in *A. aculeata* have been reported. These are based on tetrazolium tests, endogenous vitamin E content, defense-related phytohormones, oxidative stress, and morphological changes of the embryo (Barreto et al. 2014; Bicalho et al. 2015; Ribeiro et al. 2010, 2012b). Observations indicate that germination follows an asynchronous pattern and is complete when elongation of the cotyledonary petiole partially displaces the operculum (Bicalho et al. 2015; Mazzottini-dos-Santos et al. 2017, 2018).

Seed dormancy is a critical aspect in the study of acrocomia seed germination. Contrary to an initial hypothesis, endocarp hardness is not the direct cause of seed dormancy, as the endocarp has a germination pore, which allows external fluxes of water and gases to the seed (Mazzottini-dos-Santos et al. 2015b; Reis et al. 2012). Nevertheless, the endocarp limits germination under natural conditions and the effects of pre-germination treatments on seeds due to obstruction of the germination pore (Carvalho et al. 2015; Mazzottini-dos-Santos et al. 2015a, b; Ribeiro et al. 2011). Seed dormancy is explained by the interaction between embryo growth capacity and the physical resistance to displacement of tissues adjacent to the embryo (Carvalho et al. 2015; Mazzottini-dos-Santos et al. 2018; Ribeiro et al. 2011, 2012b, 2013, 2015). Mazzottini-dos-Santos et al. (2018) and Ribeiro et al. (2012b) observed slight embryo growth within non-germinated seeds of *A. aculeata*, directly associated with subsequent germination (). These findings suggest the absence of morphological dormancy and the possible existence of non-deep physiological dormancy. Mazzottinni-dos-Santos et al. (2018) evidenced embryonic growth inside non-germinated seeds until natural removal of the operculum, which could be interpreted as an indicator of morpho-physiological dormancy. This could be caused by incomplete development of the embryo, its small size in relation to the seed and adjacent layers, and the need for growth prior to germination (V. S. Carvalho et al. 2015; Díaz-Lezcano et al. 2018; Mazzottini-dos-Santos et al. 2018). More evidence is required with regard to factors that may explain a potential morpho-physiological dormancy in acrocomia (Mazzottini-dos-Santos et al. 2018). Moreover, dormancy may also vary between populations (V. S. Carvalho et al. 2015).

The complexity of dormancy implies the need for combined pre-germination treatments (Ribeiro et al. 2011). A number of methods have been proposed to overcome seed dormancy by displacing the seed tegument layer and stimulating embryonic growth. Observations indicate that mechanical removal of the operculum contributes to breaking seed dormancy and has higher effectiveness on germination than gibberellic acid (Bicalho et al. 2015; Mazzottini-dos-Santos et al. 2018; Ribeiro et al. 2011, 2015; Rodrigues Junior et al. 2013; Rubio Neto et al. 2014). The latter stimulates embryonic growth, induces longer-term germination, and possibly contributes to weakening the operculum and reducing oxidative stress during germination (Bicalho et al. 2015; Carvalho et al. 2015; Mazzottini-dos-Santos et al. 2018; Ribeiro et al. 2011, 2015; Rubio Neto et al. 2014). Weakening of the adjacent tissues is also induced by imbibition in water; however, physical restriction from the opercular seed coat constrains germination (Mazzottini-dos-Santos et al. 2018). It was found that this layer does not impede water uptake, therefore indicating the absence of physical dormancy (V. S. Carvalho et al. 2015; Rodrigues Junior et al. 2013). Germination control factors include the variation in cell wall pectins in the micropylar endosperm (Mazzottini-dos-Santos et al. 2018). Additionally, metabolic activity and mobilization of reserves favor germination and are driven by enzymatic and hormonal processes (Bicalho et al. 2015, 2016; Mazzottini-dos-Santos et al. 2018; Ribeiro et al. 2015). Metabolic activity could be also influenced by higher oxygen availability after removal of the operculum (Ribeiro et al. 2015).

A pre-germination protocol patented by Motoike et al. (2007) (Patent register PI0703180-7) encompasses seed extraction from the endocarp, sterilization, imbibition, mechanical removal of the operculum, and application of growth regulators (i.e., gibberellic acid), saline, and oxidizing solutions (Bicalho et al. 2016). Application of this protocol exhibited an 80% (±5%) germination rate three days after removal of the operculum and sowing (Bicalho et al. 2016). Germination rates of around 65% were reported for seeds without operculum 20 days after sowing, increasing to approx. 80% when the opercular seed coat was removed (Mazzottini-dos-Santos et al. 2018). In contrast, treating intact seeds with gibberellic acid resulted in germination rates of 60% and germination taking three times longer (Mazzottini-dos-Santos et al. 2018). Combination of these procedures resulted in mean germination rates higher than

50% within two weeks (Berton et al. 2013; Ribeiro et al. 2011). Frequent application of lower concentrations of growth regulator may increase germination rates (Berton et al. 2013; Oliveira et al. 2013). Temperature also influences germination. This was observed by Machado et al. (2015) for *A. totai* seeds at temperatures varying from 25 to 35 °C. However, they also found that high temperatures lead to seed contamination. Seasonal thermal variation from winter to spring promotes the germination of soil seed banks and seedling emergence at the beginning of the warm rainy season (Rodrigues-junior et al. 2016; Souza et al. 2019b). A study by Ribeiro et al. (2012a) and Rodrigues-Junior et al. (2016) concluded that stratification of seeds in most conditions at 35 °C for 60 days can promote germination. Pre-germination using thermal shocks (70 °C) and long-duration heat treatments (35–40 °C) do not significantly stimulate the germination of seeds without endocarp and could decrease their viability. Storage conditions also influence the viability of the seed. In fact, temperatures between 15 and 20 °C and a moisture content between 6 and 8% enhance germination rate up to 84% in *A. aculeata* seeds along storage period as observed for a period of twelve months (de Souza et al. 2016). Seed aging leads to loss of viability and deterioration of lipids and membrane, primarily caused by high moisture content, high temperatures, or extensive drying processes (Barreto & Garcia 2017; Neto et al. 2012).

3.4.4.6 Seedling development Seedling development consists of six phases that last approximately 150 days in total, from germination until observable growth of taproot, shoot, and haustorium. Once germination is completed, the cotyledonary petiole elongates, increasing enzymatic activity and growth of the haustorium, which controls mobilization of seed reserves (i.e., protein, lipid and polysaccharide reserves, and cell wall components) (Bicalho et al. 2016; Mazzottini-dos-Santos et al. 2017). Water content increases with seedling development, reaching a maximum in phase III, in which the cotyledonary petiole also reaches its maximum length (Mazzottini-dos-Santos et al. 2017). Temporary accumulation of dry matter (i.e., starch) in the haustorium indicates the mobilization of seed reserves, which intensifies in phase IV (Bicalho et al. 2016; Mazzottini-dos-Santos et al. 2017). These are converted into carbohydrates by the haustorium and then transported to the vegetative axis (Mazzottini-dos-Santos et al. 2017). The development of the latter is associated with high concentrations of salicylic acid and jasmonic acid (Ribeiro et al. 2015). Further biochemical studies are required to expand the knowledge of pathways and reactions at cellular level in the haustorium (Mazzottini-dos-Santos et al. 2017). Different activity levels of hydrolytic enzymes in endosperm and haustorium suggest that the former does not exclusively store reserves (Bicalho et al. 2016; Mazzottini-dos-Santos et al. 2017). The last phases exhibit an increase in growth of the shoot, taproot, and haustorium, as well as a reduction in water content (Mazzottini-dos-Santos et al. 2017). Acrocomia seedlings develop a tuberous underground system (i.e., saxophone stem structure) that stores reserves and results from the growth, curvature, and expansion of the embryo (Souza et al. 2017b). This structure influences the distribution of the root system (Moreira et al. 2019).

Under natural conditions, the emergence of *A. aculeata* seedlings was found to be synchronized with the rainy season (Souza et al. 2019b). Seedling production consists of two stages prior to field planting (1-year-old plants): 1) pre-nursery stage of pre-germinated seeds until formation of first pair of split leaves and 2) nursery stage until emergence of second pair of mature leaves (Pimentel et al. 2016). Observations indicate that the hardening procedure at pre-nursery stage, used to increase robustness of seedlings, does not enhance the acclimation response and therefore its application would not be favorable (Dias et al. 2018). Organic–mineral substrate mixtures are suitable for commercial seedling production due to their physical structure (Costa et al. 2014; Pimentel et al. 2016). Manure provides good conditions for root growth and plant total dry phytomass value (Costa et al. 2014; Pimentel et al. 2016). In general seedlings respond well to treatments with soil conditioners and fertilizers, although no significant differences in terms of plant traits (e.g., plant height, stem diameter, number of leaves, shoot dry matter, leaf area index, and root dry matter) were found when applying different organic and chemical fertilizer treatments (Machado et al. 2016; Pimentel et al. 2016). Observations indicate that the combined application of chemical fertilizers and soil conditioners on clayey and sandy soils increases nutrient levels of *A. aculeata* seedlings' leaves and soils, as well as soil organic matter and microbial biomass carbon (Machado et al. 2016). Quarterly top dressing and surrounding with a thermo-reflective screen are recommended during the nursery process (Costa et al. 2014; Pimentel et al. 2016). *A. aculeata* seedlings present different adjustment mechanisms that contribute to acclimation responses under contrasting light conditions during pre-nursery and nursery stages (Dias et al. 2018).

3.4.4.7 Micropropagation Cloning techniques have recently been applied for the production of acrocomia plantlets for cultivation. This may reduce the time required for propagation in comparison to natural reproduction by seed (Granja et al. 2018), once suitable protocols are established. Accordingly, somatic embryogenesis has been applied for *A. aculeata* multiplication. Zygotic embryos have been primarily used as explant source, which has contributed to the knowledge of their morphology and anatomy during micropropagation phases (Granja et al. 2018; Moura et al. 2008, 2009, 2010; Ribeiro et al. 2012b). The first reported protocol on somatic embryogenesis using zygotic embryos from *A. aculeata* allowed the attainment of somatic embryos as explant source (Moura et al. 2009). This protocol has been further improved with the aim of attaining more efficient somatic embryos development and maturation. Consequently, various exogenous plant growth regulators have been applied under different conditions (Fernández et al. 2016; Luis & Scherwinski-Pereira 2014; Soares et al. 2011). Improvements in culture media formulation have resulted in high effectiveness of callus formation and enhanced development and germination of somatic embryos (Granja et al. 2018). Cloning, however, means that the material is clonal to each other but not necessarily to the mother plant as acrocomia is an open-pollinating species. Overall, the cycle from incubation of the zygote embryo until embryogenic callus lasts about 180 days, demanding less time than other protocols (Granja et al. 2018; Luis & Scherwinski-Pereira 2014). Granja et al. (2018) concluded that the responsiveness of zygotic embryos to somatic embryogenesis varied by matrix, suggesting that if micropropagation is to be used as a mass propagation technique for this species, the genotype of the explant has to be considered. In embryo culture, limitations of haustorium, root, and leaf development contribute to low acclimatization capacity of seedlings. According to Vieira et al. (2020), incorporating organic substances into the culture medium found in the endosperm, being hormonal stimulus for root development, as well as autotrophic culture may improve the acclimatization of *A. aculeata* seedlings. Additional gains of micropropagation include high multiplication rates of embryogenic lines and the maintenance of a continuous multiplication cycle (Granja et al. 2018).

Research on storage conditions suggests that keeping fruits in a temperature range of 10 to 27 °C favor embryo viability (Bandeira et al. 2013; Barreto et al. 2014; Ribeiro et al. 2012a). Other studies recommend different preservation methods of fruits and zygotic embryos (Luis & Scherwinski-Pereira 2017). In addition to external variables, such as culture media, somatic embryogenesis is also affected by intrinsic factors such as genotype. In fact, variation in in vitro responsiveness of open-pollinated families of *A. aculeata* are possibly attributed to genetic differences (Granja et al. 2018).

Other explant sources tested for somatic embryogenesis include leaf tissues from in vitro-cultured young plants, applying the Thin-Cell Layer technique (Padilha et al. 2015), and from adult plants (Meira et al. 2019). Results show the potential of obtaining somatic embryos from these tissues, although advances in conversion rates are still necessary (Padilha et al. 2015). Continued research efforts are required to increase the effectiveness of plantlet regeneration and to further understand and optimize the mechanisms involved during micropropagation processes (Granja et al. 2018; Moura et al. 2010).

3.4.5 Cultivation systems and crop management

Existing value chains based on acrocomia still rely on fruits collected by small-scale farmers from natural populations and either supplied to local small-scale oil extraction facilities mainly for cosmetic applications or processed on-farm by local communities for diverse food applications (Cardoso et al. 2017; de Lima et al. 2018; Lopes et al. 2013; Plath et al. 2016; Vargas-Carpintero 2018). Commercial cultivation of *A. aculeata* and the derived value chains are at an early stage of development (Plath et al. 2016). Since 2016, two projects have established large plantations of 1000 and 760 ha of *A. aculeata* in the state of Minas Gerais (Brazil) (Colombo et al. 2018; Evaristo et al. 2018; INOCAS 2020). The 760 ha plantation, led by a private company, implements an outgrower scheme primarily with small farmers (average farm size 58 ha). It uses *A. aculeata* genetic material from natural populations possibly selected based on morphological traits to establish the plantations on degraded pastures with an agroforestry approach (CIF 2020; INOCAS 2020). Similarly, a community-based project in the region of San Pedro del Paraná (Paraguay) promotes the cultivation of *A. totai* through adoption by small-scale farmers (< 2 ha plantation area per farmer) with the goal of establishing 250 ha intercropping with annual crops (Mössinger 2020; Vargas-Carpintero 2018).

3.4.5.1 Cultivation systems The cultivation of *Acrocomia* spp. as a native palm genus in diversified land-use systems has been stated as a potential route to the establishment of sustainable production systems in terms of socio-economic, environmental, and biophysical dimensions (Alfaro-Solís et al. 2020; Cardoso et al. 2017; Motoike et al. 2013). Accordingly, one possible cropping system for acrocomia is its integration with cattle farming, i.e., silvopastoral systems, on extensive pasture areas such as those in the savannah region of Brazil (Cerrado) (Plath et al. 2016). This may potentially allow the rehabilitation of cattle lands and the diversification of products for farmers. Current experience on the establishment of silvopastoral and agrisilvicultural systems with *A. aculeata* has been reported in the region of Minas Gerais (Brazil) at three planting densities: 400, 312, and 192 palms per hectare (CIF 2020; Imaflora 2020).

Dispersed acrocomia palms are found in managed pastures in tropical dry ecosystems of Latin America (Esquivel-Mimenza et al. 2011; Plath et al. 2016). Relationships between *A. aculeata* and pastures indicate that harvest of standing herbage biomass underneath these palms is higher than for other tree species. Compared to open pastures, herbage biomass yields under *A. aculeata* show only a slight reduction or even slight gain (Esquivel-Mimenza et al. 2013; Villanueva et al. 2008). This is favored by the high photosynthetic active radiation underneath *A. aculeata*

(50–70% of full sun). Various biomass quality indicators are also enhanced by shading, especially protein content of pasture (Esquivel-Mimenza et al. 2013). Positive effects on soil properties were also evidenced by intercropping *A. aculeata* with pastures, particularly organic carbon content and microbial biomass (Leite et al. 2013). The setting-up of silvopastoral systems using *A. aculeata* requires specific grazing practices during plantation establishment and production cycles (Barbosa et al. 2009; CIF 2020). Commonly, cattle under natural Acrocomia groves consume the fruits and leave the nuts on the ground. These are occasionally collected and sold on to local processing facilities (Esquivel-Mimenza et al. 2011; Vargas-Carpintero 2018).

Intercropping *A. aculeata* with perennial crops such as coffee at varying planting densities has been found to result in higher coffee yields than in unshaded cultivation systems, in particular at the moderate distance between plants (Moreira et al. 2018). The authors concluded that intercropping contributes to modifying the microclimate of the coffee plants and that a higher density of palms results in higher soil moisture content (Moreira et al. 2018). Moreover, the shading effect provided by acrocomia was more influential than the competition for water between the two cultures (Moreira et al. 2018). In addition to perennial crops, a number of seasonal crops have been intercropped with acrocomia including pineapples, beans, sweet potatoes, cassava, pumpkin, rice, corn, watermelon, peanuts, and sunflower (Céspedes de Zárate 2015; CIF 2020; J. Corrêa et al. 2018).

Outside of the inner tropics, most suitable areas for the cultivation of *A. aculeata* (based on a set of environmental predictors) can be allocated within savannahs of: a) Central America and northern regions of Colombia and b) Venezuela, southern Brazil, and eastern Paraguay (Plath et al. 2016). De Lima et al. (2018), on the other hand, indicate that many natural acrocomia habitats are found in western and central Brazil, where savannahs are abundant. Results from an agroclimatic zoning model indicate that north and northeast Argentina are also suitable (Falasca et al. 2017). Similar predictions are available for Brazil suggesting the importance of the entire natural occurrence area of *A. aculeata* for exploring its productive potential (Resende et al. 2020). Plath et al. (2016) found that 2.8% of the potential area (3.7 M km^2 under present climate conditions) is considered highly suitable by the modeling study and 37.1% moderately suitable. Savannah and combined forest areas account for 42.6% and 21.2%, respectively. However, many of these areas have a high conservation value, implying environmental burdens (Plath et al. 2016). The authors estimate that under 'business-as-usual' climate change scenarios, more than half of these potential cultivation areas would be unsuitable in the long term and this would increase the pressure on dry forests (Plath et al. 2016).

There is still huge uncertainty regarding growth and yield performance of acrocomia in plantations. Applying a modeling approach to identify most suitable cultivation practices, considering site-based biophysical factors may help to close knowledge gaps on its cultivation in suitable integrated land-use systems. The *Water, Nutrient, Light Capture in Agroforestry Systems* model allows capturing tree–soil–crop interactions at plot level under a wide range of environmental conditions (Hussain et al. 2015; Radersma et al. 2005; Suprayogo et al. 2002; van Noordwijk & Cadisch 2002; van Noordwijk & Lusiana 1998), enabling evaluation of management options based on site-specific information.

3.4.5.2 Crop management The root system of *A. aculeata* follows a radial spreading pattern that corresponds to the crown projection area (Moreira et al. 2019). The authors found a higher proportion of roots at the superficial level, mostly concentrated in the tuberous region during the first years. At adult phase, roots distribute uniformly, with a higher density near the stem and a higher effective depth (Moreira et al. 2019). These findings indicate which areas should be preferably targeted by fertilizing and irrigating activities. Additionally, they suggest that the planting layout should follow a specific spatial orientation (Moreira et al. 2019).

Fertilization using the side-dressing method has been tested in *A. aculeata* at a juvenile stage of development (< 2 years). It showed a positive plant response to increasing rates of N and K and variability among genotypes' nutrient use efficiency (Pimentel et al. 2015). Analysis of nutrient content indicated that increasing rates of N and K only influenced K content of leaves with no changes in micro- and macronutrient contents being observed (Pimentel et al. 2015). However, variation in nutrient content according to leaf age and position should be also considered (Pimentel et al. 2015; Pires et al. 2013). Field data from an *A. aculeata* plantation show that around 4 t ha^{-1} lime is applied during establishment and less than 1 t ha^{-1} per year after the second year (Evaristo et al. 2018). These values depend on soil analysis and previous land use. Fertilization increases with time, from 0.37 t ha^{-1} in the first year up to 2.1 t ha^{-1} at 10 years (Evaristo et al. 2018). Further information about nutrient demand in different growth stages is required (Pimentel et al. 2015).

Rainfall interception and high stem flow in *A. aculeata* palms enable water infiltration and minimization of erosive processes (Corrêa et al. 2016). Soil erosion in A. *aculeata* steep cultivation systems could be further prevented by implementing narrow-base terraces, a soil conservation technique to reduce surface runoff (Corrêa et al. 2018). Further studies on soil conservation considering intercropping are required.

Despite there being no evidence of pests or diseases in commercial plantations of acrocomia (César et al. 2015; Colombo et al. 2018), potential threats have been identified in a number of studies, contributing to the planning of integrated pest management during cultivation and post-harvest. These threats include phytophagous scarabs that feed on flowers and roots, the red palm mite, lethal yellowing disease caused by phytoplasma bacteria, fungal pathologies, and seed predator insects that attack mature fruits (Guatimosim et al. 2012; Maia et al. 2018, 2020; Pereira et al. 2014; Ramos et al. 2001; Roca et al., 2006; Souza et al. 2020; Zuart-Macías et al. 1999). Based on agricultural practices, around 10 kg ha^{-1} agrochemicals including pesticides and herbicides are applied during the first year of establishment and 2.2 kg ha^{-1} per year after the fifth year (Evaristo et al. 2018). Infestation with triatomine species, particularly of the genus *Rhodinus*, has been documented for large palms, among them *A. aculeata* (Abad-Franch et al. 2015; Ricardo-Silva et al. 2012; Rodriguez & Loaiza 2017). As these bugs transmit *T. cruzi* (Chagas disease), control mechanisms are highly relevant for preventing infestation and human disease in the surroundings of cultivation areas (Abad-Franch et al. 2015; Ricardo-Silva et al. 2012).

Various methods for harvest optimization have been tested. The mechanical properties of the fruit-rachilla system of *A. aculeata* have been explored for developing harvesting machines based on mechanical vibration (Grupioni et al. 2018, 2020; Velloso et al. 2017; Villar et al. 2017). Methods of monitoring fruit maturity include optical analysis using the biospeckle laser technique and image processing, which assesses features such as fruit volume and color (Costa et al. 2016, 2017, 2018c).

3.4.5.3 Productivity Fruit and oil yield estimations are usually calculated on the basis of adult palms from natural populations and biometric traits and oil content of their fruits. Ciconini et al. (2013) estimated the fruit yield of *A. aculeata* based on adult palms of unknown age at various locations in the Cerrados and Pantanal regions of Brazil with a high plant density of 1000 palms ha^{-1}, equivalent to a row spacing of 2 m × 5 m. The authors projected a fresh fruit yield ranging from 13.7 to 25.5 t ha^{-1} (6.1–12.2 t pulp and 0.7−1.2 t kernel). Considering 400 palms ha^{-1} (spacing of 5 m × 5 m, suitable for agroforestry) gave a maximum productivity of 10.2 t fresh fruits, which corresponds to individual palms located in the Cerrado biomes (Ciconini et al. 2013). Projections based on the average yield of palms from Minas Gerais (Brazil) indicate an annual productivity of 23.2 t ha^{-1} fruit dry matter with a plant density of 400 palms, which doubles to 46.1 tons when considering the average yield of the most productive plants (Evaristo et al. 2016a, 2018). Lower plant densities have also been used for productivity estimations, such as 200 palms ha^{-1} with a projected productivity of 8.8 t pulp and 1.9 t kernel (Sanjinez-Argandoña & Chuba 2011).

Average yields of 2.9 t pulp oil and 0.5 t kernel oil per hectare have been projected for *A. aculeata* fruits in Minas Gerais (Brazil) based on a plant density of 400 palms ha^{-1} (Evaristo et al. 2016a). In a high-yield scenario, up to 5.7 t pulp oil and 1 t kernel oil per hectare have been estimated at the same plant density (Evaristo et al. 2016a). In contrast, Ciconini et al. (2013) projected average yields ranging between 0.26 and 0.44 t pulp oil and 0.1 and 0.18 t kernel oil of *A. aculeata* fruits in the Cerrado and Pantanal regions (Brazil), assuming a mechanical extraction efficiency of 70% and 400 palms ha^{-1}. Considering the individuals with highest yields, 1 t pulp oil and 0.4 t kernel oil could be obtained at the same plant density and same extraction rate (Ciconini et al. 2013). The large variability in productivity estimations leads to a high degree of uncertainty and is a result of the natural variability of native stands, the lack of accurate information on plant age, and the absence of data from older plantations. Additionally, further studies on productivity under silvopastoral and agrisilvicultural scenarios and appropriate agronomic management are required (Ciconini et al. 2013). There is also lack of studies comparing these integrated productions systems with monocropping. Using land equivalent ratios and AreaxTime equivalent ratios may help to identify best cropping practices.

3.4.5.4 Environmental and social impacts Modeling the global warming potential associated with the production of *A. aculeata* results in emissions of 141 kg CO_2eq. per ton fruit for a timeframe of 100 years, assuming a productivity of 30 t fruits ha^{-1} year and a plant density of 460 palms ha^{-1} (excluding land-use change impacts) (Fernández-Coppel et al. 2018). Cultivation activities account for 93% of these emissions, with fertilization (mainly N fertilization) having the highest influence (90%) (Fernández-Coppel et al. 2018). A similar study on *A. aculeata* found total emissions of around 216 kg CO_2eq per ton fruit (181.4 t CO_2 ha^{-1}) for a time horizon of 30 years, assuming a productivity ranging from 27 to 46 t fruits ha^{-1} year and including impacts from conversion of grassland into cropland (Evaristo et al. 2018). According to the authors, land-use change accounts for 23.4% of estimated greenhouse gas emissions, without considering cultivation on degraded land. Total emissions per ton of *A. aculeata* fruit are similar to values reported to African oil palm fresh fruit bunches when excluding land-use change (Fernández-Coppel et al. 2018). However, when compared to cultivation of African palm oil on rainforest or grassland converted into cropland (i.e., integrating emissions from land use change), acrocomia would have a positive performance in terms of greenhouse gas emissions (Fernández-Coppel et al. 2018). Given the accumulation of carbon in *A. aculeata* palms above and below ground, it is estimated that 28.73 t CO_2 eq ha^{-1} could be sequestrated per year (plant density 400 palms ha^{-1}) (Moreira et al. 2019). Estimations of the emission balance of *A. aculeata* in a timeframe of 30 years result in a negative value (more carbon sequestrated than emitted) ranging from -617 to -956 t CO_2eq ha^{-1} (Evaristo et al. 2018; Imaflora 2020). This suggests a potential advantage in comparison to the emission balance of African oil palm cultivation (Germer and Sauerborn (2008) estimated that the emission balance of African oil palm ranges from -136 to -1335 t CO_2 eq ha^{-1} depending on crop management and land-use change) (Evaristo et al. 2018; Moreira et al. 2020b).

Estimations of socio-economic effects suggest that acrocomia could generate more employment in the Brazilian primary sector than alternative perennial crops used for production of jet biofuels such as sugarcane and eucalyptus (Wang et al. 2019, 2018). Similarly, an analysis of various midpoint impacts associated with human health indicates that acrocomia-based jet biofuel performs better than that from the crops mentioned above and fossil jet fuels (Wang et al. 2020). The authors estimate that primary production of *A. aculeata* accounts for a large proportion (25%) of total human health impacts. Despite a high uncertainty, a positive contribution of acrocomia jet biofuel value chains to Gross Domestic Product is foreseen (Wang et al. 2019, 2018). The *ex ante* analysis offers a baseline for the anticipation of risks, especially with regard to potential hotspots such as work accidents, employment of women, and informal labor (Wang et al. 2018). Further studies are required to anticipate potential impacts on diverse stakeholders, primarily farmers (Marting Vidaurre et al. 2020), taking into consideration additional impact categories such as livelihood, food security, energy security, land rights (Wang et al. 2018), social values, and participatory approaches (González-Marín et al. 2012). Moreover, potential human health risks associated with acrocomia should be included in impact assessments (Abad-Franch et al. 2015; Ricardo-Silva et al. 2012).

4 Acrocomia, ballyhooed or still neglected?

This review has explored the accumulated knowledge on *Acrocomia*, evidencing that this genus is being increasingly studied from interdisciplinary perspectives. Fundamental and applied research, particularly on *A. aculeata*, have advanced significantly during the last two decades, driven by its potential as a source of vegetable oil for the biofuel sector. Thus, from a scientific point of view we conclude that, this palm is far from being neglected. Interest in the use of fruit fractions for a variety of applications has led to exponential growth in the number of studies on this palm, underlining its multipurpose features and potential value in bioeconomy. Its ecological plasticity, physiological capacity, and high productivity enable acrocomia to adapt to a range of environments outside tropical rainforests, thus providing tremendous scope for sustainable widespread cultivation. While keeping in mind the need for a cautious and systemic approach to avoid an 'acrocomia hype,' this review provides a wealth of detail on the accumulated knowledge that has contributed to the domestication of this plant and its preparedness for sustainable biomass supply.

Looking at the genus as a whole, it appears evident that only a few species have been widely studied, while others remain largely neglected. Further studies on its taxonomic classification are thus necessary. To date, *A. aculeata* is the most investigated species and could serve as a model for other species such as *A. totai*. The body of knowledge relating to the botany and crop development of *A. aculeata* is diverse and includes information on genotypic diversity, cross-regional biometric characterization, phenotypic plasticity, and plant adaptability. Additionally, characterization of its reproductive biology and genetics has contributed to a better understanding of this species. Key resources and tailored technologies for germination and propagation have already been established, encompassing germplasm banks and molecular biology information. Input data to assist breeding programs, crop development, and agronomic practices have also been generated. Research on genotypic and environmental variability indicates that morphological variation is predominantly determined by genetics. Further cross-regional studies on the influence of environmental factors on plant adaptability, productivity, and biomass quality are required.

The knowledge accumulated in the last 14 years, particularly breakthroughs in germination, propagation, and seedling development, represents significant advances in the domestication and cultivation of *A. aculeata*. These have promoted its preparedness, resulting in initial plantations (Fig. 5). So far, there are no commercial varieties of acrocomia, indicating that first plantations are still based on wild planting material, which has not been subjected to genetic improvement. As such, *A. aculeata* can currently be considered a semi-domesticated plant partially prepared for the market. Fruits are marketable for a wide spectrum of material and energetic applications based on pulp and kernel oils and the remaining fruit fractions, i.e., press cakes, endocarp, and epicarp.

The findings suggest that this palm species has already departed its role as a purely non-timber forest natural resource and is on the way to becoming a new plantation crop with high potential for the bioeconomy. However, the high level of uncertainty associated with agronomic practices, plant productivity, and biomass quality exposes the need for accompanying research. For full domestication and prompt establishment of acrocomia value chains and webs, there is a demand for breeding programs to provide improved varieties tailored to a range of edaphic conditions and environmental factors. Technologies have been approved for the identification of elite material but concentrate primarily on *A. aculeata*. Other species such as *A. totai*, with intrinsic value as a local genetic resource in other Latin American biomes, still require substantial efforts to advance crop development and conservation strategies. This could lead to diverse territorial bioeconomy systems, supporting forest landscape restoration. In Paraguay and Costa Rica, first small-scale plantations of *A. totai* using wild planting material are at early stage of development.

Such initiatives face high risks of failure and uncertainty—common characteristics of novel crops in the process of domestication and market development. For instance, there is high variability and uncertainty related to genetic and environmental factors that affect biomass quality and productivity. Therefore, inter- and transdisciplinary research with a systemic perspective and a site-based approach is crucial for the reduction of technical (e.g., ecophysiological requirements, agronomic practices, crop development) and non-technical challenges (e.g., governance, farmer adoption, and risks) to ensure successful introduction and sustainable implementation of acrocomia as an alternative crop. In this context, decision support tools need to be enhanced and developed at farm (Mössinger 2020), meso- and macro-level, which allow the productivity of acrocomia-based cropping systems to be estimated. An *ex ante* analysis using a modeling approach that covers a wide range of management options and environmental conditions would help to identify best agronomic practices based on already existing data and lead to regionally tailored cropping patterns. This may provide information not only on acrocomia's growth performance but also on its environmental impact, carbon sequestration, and resilience in the context of integrated copping systems or nature-based solutions. In this way, interaction between crop development targets and agronomic practices could be oriented toward multiple objectives related to plant adaptability, efficiency, and positive environmental performance. Comparisons of scenarios using different oil crops would also allow informed decision-making and promote future sustainable vegetable oil production. In addition to a systemic value web analysis from the supply of acrocomia fruits through to the final products, future research must incorporate context-dependent environmental and social aspects to guarantee a truly sustainable supply of acrocomia, providing a blueprint for the sustainable use of local biodiversity.

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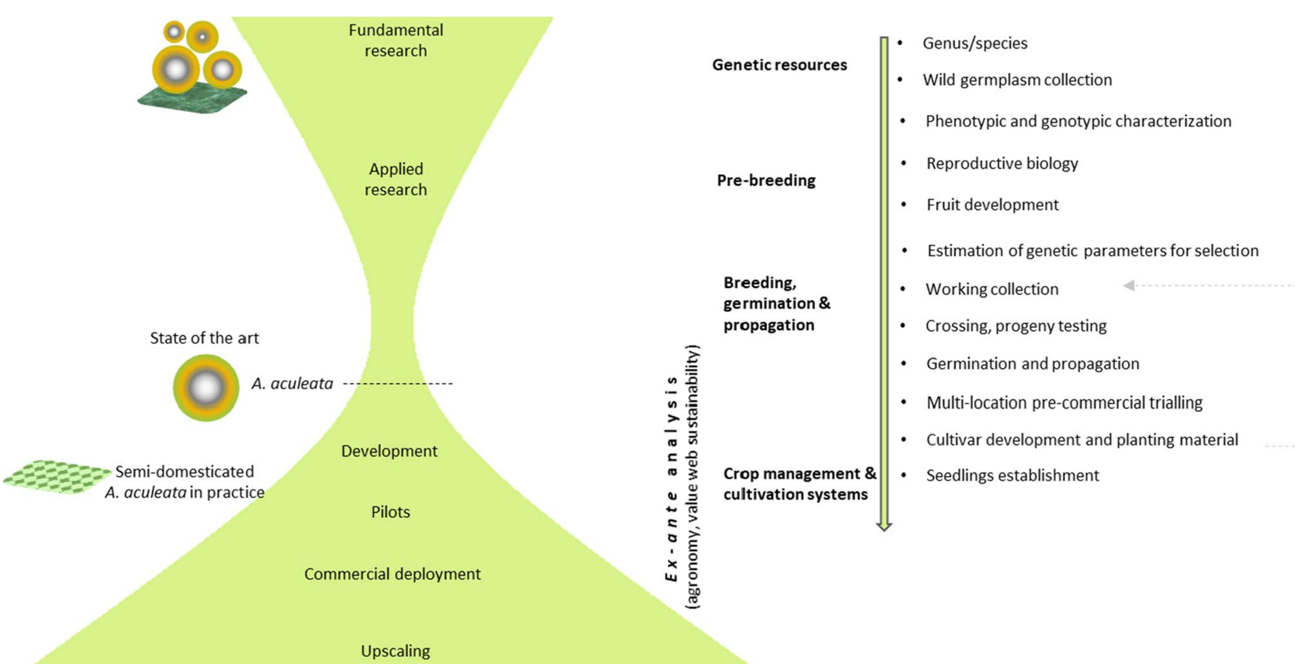

Fig. 5 Status of acrocomia, specifically *A. aculeata*, in the crop development process from fundamental research to commercial deployment and up-scaling (adapted from Clifton-Brown et al. 2019; Sharma 2017).

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