Journal of Tropical Biology and Conservation 15: 61–80, 2018 ISSN 1823-3902
E-ISSN 2550-1909

Research Article

Jackfruit (*Artocarpus heterophyllus*) and Breadfruit (*A. altilis*): Phytochemistry, Pharmacology, Commercial Uses and Perspectives for Human Nourishment

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Abstract
The *Artocarpus* J. R. & G. Forster genus is comprised of about 50 species. *Artocarpus* is derived from the Greek word *artos*, meaning bread while *karpos* means fruit. There are two species that are widely distributed in tropical regions, *Artocarpus heterophyllus* Lam., known as jackfruit, and *Artocarpus altilis* (Parkinson) Fosberg, known as breadfruit, both in the Moraceae or mulberry family. Both of these *Artocarpus* species have medicinal properties and biological activities that are derived from almost every part of the tree, fruit, seed, wood, bark, leaves and sap. This review examines the limited work that has been conducted on the biology and biotechnology of these two *Artocarpus* species with the hope that this knowledge may spur further basic and applied research.

Keywords: fruit, medicine, Moraceae, secondary metabolites, tropical tree

Introduction
The genus *Artocarpus* (Moraceae), which contains food-producing plants that are spread throughout tropical and subtropical regions of the world, consists of about 50 species (Motley, 2014), but The Plant List (2018) lists 193 accepted names for *Artocarpus*, although many of them are synonymous and unresolved species. The word *Artocarpus* is a compilation of two Greek words, *artos*, which means bread, and *karpos*, which means fruit (Jones et al., 2011).

Received 30 May 2017
Reviewed 04 October 2017
Accepted 13 October 2017
Published 15 October 2018

The species epithet of jackfruit, *heterophyllus*, is a compilation of two Greek words, *hetero*, meaning different, and *phyllus*, which means leaf (Gupta, 2011). This implies existing variation in the shape and size of the leaves. Jackfruit, which typically grows in the form of a tree, provides edible fruit and medically potential secondary metabolites, is a source of timber, and has been cultivated throughout China, Sri Lanka, India and Southeast Asia, but is also found in Africa, the Caribbean islands, Brazil, Suriname and tropical parts of Australia (Thaman & Ali, 1993). Jackfruit is known as *nangka* in Indonesia and has various ethnobotanical properties that derive from its ripe fruit which serve as ingredients for local sweets such as *kolak* and *dodol* in Java, young fruit is consumed as a vegetable, and its leaves are used as cattle feed (Lim, 2012). Ash of leaves can be used to treat wounds and serve as medication to treat ulcers (Gogte, 2000). Jackfruit timber is a good wood for furniture, construction material, and musical instruments since it resists bacterial, fungal and termite attacks (Orwa et al., 2009).

The methanolic extract of stem, root bark and heartwood, leaves, fruit, and seed have multiple antibacterial compounds (Khan et al., 2003). One of those compounds, artocarpin, is used as an antitermite agent (Shibutani et al., 2006). The basal part of the fruit, which is fleshy, fibrous and rich in sugar, provides a good natural source of carbohydrates and minerals such as calcium, iron, magnesium, carboxylic acids, and vitamins A, C and E, primarily ascorbic acid and thiamine (Rahman et al., 1999). Mature seed are edible when dried or after cooking by boiling and roasting. Fresh mature seed contain 25 IU/100 g of vitamin A, 4.3-6.6 g/100 g of protein, 23-25 g/100 g of calcium, 80-126 mg/100 g of phosphorus, and 10-17 mg/100 g of ascorbic acid (Acedo, 1992). In fresh (raw) fruit, there are 23.25 g/100 g of carbohydrate, 24 mg/100 g of calcium, 0.23 mg/100 g of iron, 29 mg/100 g of magnesium, 110 IU/100 g of vitamin A, 13.7 mg/100 g of vitamin C (ascorbic acid), and 0.34 mg/100 g of vitamin E (α-tocopherol) (USDA, 2016). The latex which also has anti-syphilitic and vermifuge properties, contains 71.8% resin, 63.3% of which are yellow fluavilles and 8.5% white albanes that are useful for varnishes (Rao et al., 2014). A study conducted in New Delhi and Kerala, India by Suba Rao (1983) showed that jackfruit is symbiotically asociated with *Azotobacter* and *Beijerinckia*, 35 and 4 $\times 10^4$/g soil, respectively at pH 6.8-7.5, and 14 and 18 $\times 10^4$/g soil, respectively at pH 3.5-5.5. According to Prakash et al. (2009), a hot water extract of jackfruit leaves when consumed orally by humans at 20 g/kg of the patient's weight, improves glucose tolerance for mature-onset diabetic patients, while the crude methanolic extract of jackfruit parts (stem, root heartwood, bark, leaves, fruits and seeds) and their subsequent partitioning with petrol, dichloromethane, ethyl acetate and butanol gave fractions that exhibited broad spectrum antibacterial activity, the most active fraction being the butanolic extract of fruits and root bark. An extract from jackfruit shoots also revealed nematicidal activity against *Rotylenchulus reniformis*, *Tylenchorynchus brassicae*, *Tylenchus filiformis* and *Meloidogyne incognita* (Sharma & Trivedi, 1995 cit. Prakash et al., 2009).

The species epithet of *A. altilis*, the word *altilis* itself is a Greek word that means fat, refers to the fruit shape (Small, 2011). Breadfruit, also a source of food, was first cultivated in the Western Pacific about 3,000 years ago and is native to the eastern part of Indonesia, New Guinea, Malaysia and the Philippines (Orwa et al., 2009). The migration of Polynesians to South and South America, Africa (Senegal, Ghana, and Liberia), India, Maldives and Sri Lanka contributed to the distribution of breadfruit (Deivanai & Bhore, 2010). The breadfruit tree is often employed in a mixed cropping system with yams, banana, black pepper and coffee, although details of these cropping systems are lacking (Ragone, 1997). The fruit of ripe breadfruit can be eaten fresh or cooked by steaming, roasting and frying (Ragone, 1997). Leaves and the non-edible part of fruit can be used as cattle feed while tree bark can also serve as feed for horses (Morton, 1987). In Samoa and several Pacific Islands, bark is used to cure headaches, in Java and Malaya the toasted flower is used to treat toothache, while in the Bahamas, leaves of *A. altilis* are used to relieve headaches (Kuete et al., 2011). In Indonesia, the methanolic or dichloromethane extracts of leaves have medicinal properties and are used to cure liver cirrhosis, hypertension and diabetes (Kasahara & Hemmi, 1988; Arung et al., 2009). Similar to jackfruit, breadfruit trunk wood is good for construction and furniture, and its sap can be used to trap birds and houseflies or to treat human skin and fungal diseases (Ragone, 1997).

Jackfruit and breadfruit are tropical fruits with potential beneficial uses as food, timber and ethnomedicines, but this requires scientific testing. This paper, in a bid to expand research of these trees, and expand their sustainable use and production through biotechnological interventions, highlights their basic biology such as morphology, medicinal properties and propagation (both in classical and biotechnological approaches). In this paper, we highlight research that has been conducted on two species, *A. heterophyllus* Lam. (syn: *A. integrifolia* Linn.) or jackfruit, and *A. altilis* (Parkinson) Fosberg (syn: *A. communis* J.R. Forst & G. Forst; *A. incisus* (Thunb.) L.f.), or breadfruit.

Morphology

Jackfruit is an evergreen tree 8-25 m in height and with a trunk diameter of 30-80 cm that can live up to 100 years. Young trees grow with a conical or pyramidal canopy shape that turns into a dome-shaped canopy as the plant grows older. Canopy diameter which can reach 10 m, is close to the ground and provides dense shade (Elevitch & Manner, 2006). Wood of jackfruit is categorized as medium hardwood with a specific gravity of 0.6-0.7 (Orwa et al., 2009). When the tree ages, wood turns from yellow to red or brown. Breadfruit is also an evergreen tree 15-20 m in height and with a 1-2 m diameter trunk whose bark is smooth, thick and light-grey while wood is golden although, after exposure to air, it darkens (Ragone, 1997).

Jackfruit inflorescences sprout from a short, thick stalk and emerge from the lateral side of the main stem and thick branches (Backer & Bakhuizen, 1965). The male inflorescence forms in the axil of the apical branch with a cylindrical to conic-ellipsoid shape 2-7 cm in diameter and a 1-5 cm long peduncle with a tubular calyx that has a two-lobed apex 1-1.5 mm in diameter, pubescent texture, straight filament and ellipsoid anther while the female inflorescence has a globose fleshy rachis with a tubular calyx, lobed apex and a one-celled ovary (Zhou & Gabriel, 2006). Some parts of the male inflorescence are sterile. As in jackfruit, the breadfruit inflorescence emerges from the apical trunk (Figure 1).

Figure 1. Jackfruit young fruit (left) and mature fruit (right). White scale bar = 10 cm. Unpublished figure.

The breadfruit inflorescence has a cylindric-clavate shaped flower with a 3-6 cm long peduncle and globose or ellipsoid inflorescence shape with a diameter up to 20-30 cm. It has a tubular calyx that is pubescent, has two lobes on its apical surface and has a lanceolate-shaped lobe while the anthers are elliptic. Female breadfruit flowers have a tubular calyx, an ovoid ovary with a long style and two branches on the apex. Each flower consists of a reduced tubular perianth that covers a single stamen with a two-lobed anther on a thick filament (Sharma, 1962).

Both jackfruit and breadfruit exude a sticky white latex from the injured parts of the plant (Rahman & Khanom, 2013), and forms part of the plants' defense against herbivory (Agrawal & Konno, 2009). The phyllotaxis (i.e., leaf arrangement) of jackfruit and breadfruit is distichous or spiral with simple, leathery leaf blades with a full margin and plants are monoecious (i.e., male and female flowers on the same tree) with inflorescences growing from the main branch or trunk (cauliflory) for jackfruit but sprouting from the apex of the main branch, also where new leaves emerge, and arising from simple, pseudomonomerous ovaries as in other Moraceae species (Singh, 2016). Both jackfruit and breadfruit form a single leaf blade that is lobed, but mature jackfruit leaves become entire and lose their lobes, hence the species epithet, *heterophyllus*. The leaves of jackfruit and breadfruit have stipulate leaf types, with an ovate form for jackfruit and a lanceolate to broadly lanceolate form for breadfruit. Jackfruit leaves are spirally arranged with an elliptic to obovate leaf blade, leathery, leaf margins are lobed in seedlings but entire in mature trees, with pale green on the lower leaf surfaces displaying scattered globose to ellipsoid resin cells while the axial surface is dark green, smooth and glossy (Zhou & Gilbert, 2003) with a cuneate, subdecurrent base, firmly coriaceous, leaf size is 10-20 × 5-10 cm (l × b), the stipule is 1.5-5 cm, and the petiole is 2-4 cm long (Backer & Bakhuizen, 1965). Breadfruit leaves are also spirally arranged, elliptic in shape with a broadly cuneate or obtuse base, up to 3-7 lobed along each margin, lobes are oblong, long-acuminate – acute, the stipule is 16-20 cm long, the petiole is 2-4 cm ling, and leaves are 30-100 cm × 25-65 cm (Backer & Bakhuizen, 1965).

Jackfruit and breadfruit have a compound fruit or syncarp that is classified as a compound false fruit or pseudofruit that forms from the enlargement of the stigma, and the inflorescence is composed of 1,500-2,000 flowers attached to the fruit's axis (Jarret, 1976). The fruit of jackfruit can weigh 4.5-30 Kg and can reach 30-40 cm in length, with an oblong-cylindrical shape and dark green coloration when young that turns greenish-yellow or brownish when mature.

The fruit grows and matures on the trunk for 90-180 days (Elevitch & Manner, 2006). Some jackfruit achenes contain multiple fruits, each with a bulk composed of seed and with a waxy and soft texture, golden-yellow with a sweet and aromatic aril (Orwa et al., 2009). The fruit of breadfruit is formed from the fused flower perianth, except for the base (Reeve, 1974), young fruit is light-green but turns yellowish-green when mature, and as the fruit develops, perianths fuse, becoming the fleshy edible portion of the fruit (Ragone, 1977). When sliced, breadfruit has a white flesh composed of dense perianths (Figure 2).

Figure 2. Breadfruit: whole (left) and sliced (right). Scale bar = 5 cm. Unpublished figure.

Jackfruit seed are semi-round, light brown to brown, 2-3 cm in length and 1-1.5 cm in diameter, wrapped in a whitish seed coat/testa, and a yellow aril (Figure 3). The seed is recalcitrant and can be stored for up to a month in humid conditions (Elevitch & Manner, 2006). Adelina et al. (2014) air-dried seeds for 0 h (control) to 5 h (treatments separated by 1 h) at 28°C and 70% humidity, noticing that water content was reduced from 75.03% to 22.95%, seed respiration rate declined from 7.189 mg CO_2/kg h to 5.32 mg CO_2/kg h, and seed viability dropped after 14 days of germination from 97.33% to 24.67%. The seed of breadfruit is brown, round or obovoid in shape with a thin wall 1-2 cm thick with reduced or no endosperm, hence its recalcitrance to storage or desiccation (Ragone, 1997). Some modern bread breadfruit cultivars are seedless (Devanai & Bhore, 2010). The male inflorescence of seedless cultivars produces less viable pollen than fertile, less-seeded cultivars and only few flowers in the male inflorescence produce and release pollen (Devanai & Bhore, 2010). In seedless breadfruit cultivars, nectar is only produced in male flowers but not in female flowers (Ragone, 1997). In general, the loss of fertility in breadfruit is caused by triploidy ($2n = 3x = \sim 84$) or by sterile diploids ($2n = 2x = 56$) that result from hybridization (Ragone, 2001).

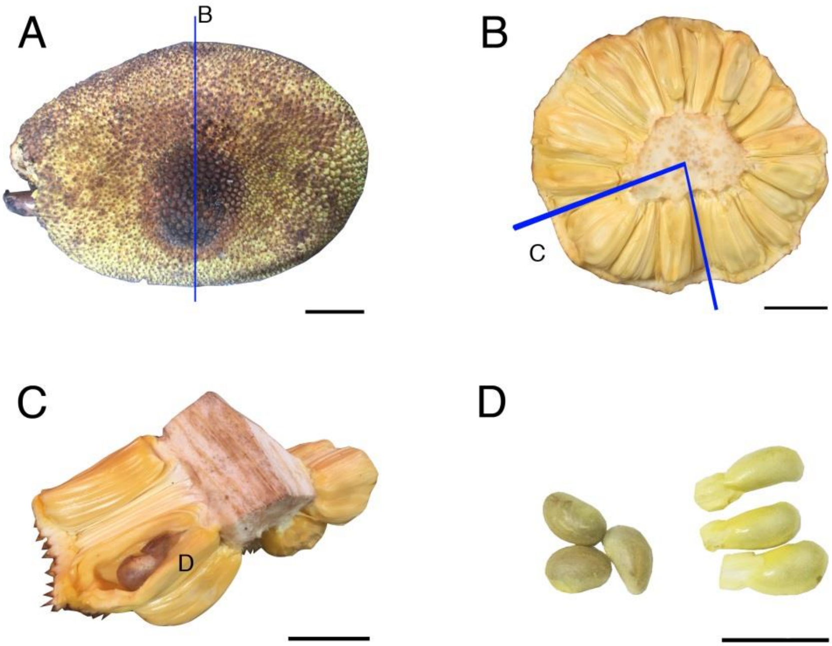

Figure 3. Mature fruit of jackfruit **(A)**, sliced **(B)**, part of the fruit with arils and the seed covered with testa **(C)**, and jackfruit seeds with testa (left) and still wrapped with aril (right). Blue lines indicate the direction of cuts. Scale bar = 5 cm. Unpublished figure.

Medicinal properties

Artocarpus produces various secondary metabolites and biologically active compounds, particularly phenolic compounds such as flavonoids (Table 1), stilbenoids, and arylbenzofurans (Hakim et al., 2006), extracted from leaves, the stem, fruit and bark, which have ethnomedicinal uses and antibacterial (Khan et al., 2003), antiviral (Likhitwitayawuid et al., 2005; 2006), antifungal towards Herpes Simplex Virus (HSV) and Human Immunodeficiency Virus (HIV) (Jayasinghe et al., 2004; Trindade et al., 2006), antiplatelet (inhibitory of thromboxane formation) (Weng et al., 2006), antiarthritic (Ngoc et al., 2005), tryrosinase inhibitory (Arung et al., 2006; Likhitwitayawuid & Sritularak, 2001) and cytotoxicity properties (Hakim et al., 2006) (reviewed in greater detail by

Table 1. Typical flavonoids, modified flavonoids, and flavonoid-derived xanthones found in *Artocarpus* (Hakim et al., 2006)

Compound class	Typical group found
Flavonoids	Chalcone Flavanone Flavone Flavan-3-ol 3-Prenylflavone
Modified flavonoids	Oxipinoflavone Pyranoflavone Dihydrobenzoxanthone Furanodihydrobenzoxanthone Pyranodihydrobenzoxanthone
Flavonoid-derived xanthones	Quinonoxanthone Cyclopentenoxanthone Xanthonolide Dihydroxanthone Cyclopentenochromone

Jagtap & Bapat, 2010). Jacalin, which is a tetrameric two-chain lectin extracted from *A. heterophyllus*, has strong mitogenic activity against human $CD4^+$ T lymphocytes, serving as an immunobiological diagnosis agent for HIV-1 patients (Kabir, 1998).

Jackfruit contains various components used for medical benefits. Some flavonoids (Table 2) are used as antinflammatory agents (Wei et al., 2005). Fang et al. (2008) extracted three phenolic compounds from the ethyl acetate fraction of jackfruit fruit: artocarpesin (5,7,2',4'-tetrahydroxy-6-ß-methylbut-3-enyl flavone), norartocarpetin (5,7,2'4'-tetrahydroxyflavone), and oxyresveratrol (*trans*-2,4,3',5'tetrahydroxystilbene). All three compounds showed a potent anti-inflammatory property after inhibiting lipopolysaccharide-activated RAW 264.7 murine macrophage cells. Other

Table 2. Flavonoids with anti-inflammatory properties (Wei et al., 2005)

Flavonoid Compounds
Cycloartomunin
Cyclomorusin
Dihydrocycloartomunin
Dihydroisocycloartomunin
Cudraflavone A
Cyclocommunin
Artomunoxanthone
Cycloheterohyllin
Artonin A and B
Artocarpanone A
Heteroflavone A, B, and C

compounds, cycloheterophyllin and artonins A and B, showed antioxidant properties as they inhibited iron-induced lipid peroxidation after exposure to oxygen radicals in more than 60% of a rat brain homogenate after the addition of 1 µM of each of the three compounds and in more than 80% when 3 µM was used (Ko et al., 1998). A chitin-binding lectin, jackin, which was purified from a saline crude extract of jackfruit seed, displayed anti-fungal properties, inhibiting the growth of *Fusarium moniliforme* and *Aspergillus niger* cultures (2.25 mg/ml, but no effect for *A. niger* at 4.5 mg/ml) and induced hemagglutination against human and rabbit erythrocytes (with at least 0.15 mg/ml) (Trindade et al., 2006). Jacalin, a 65 kDA two-chain lectin, has potential as an immunomodulatory agent, having shown mitogenicity against human $CD4^+$ T lymphocytes when added at 100 µg/ml (Blasco et al., 1995). The addition of 10, 20, 30, and 40 µg/ml of jackfruit lectin displayed *in vitro* inhibitory activity against herpes simplex virus type HSV-2, varicellazoster virus (VSZ), and cytomegalovirus (CMV) via a cytopathic effect, and inhibited HIV-1 infection *in vitro* by preventing the binding of the virus to host cells (Wetprasit et al., 2000; Swami et al., 2012).

The methanolic and ethyl acetate extracts from breadfruit fruit contain steroids, phenolics and flavonoids that can inhibit the growth of human pathogenic bacteria like *Enterococcus faecalis*, *Staphylococcus aureus*, *Streptococcus mutans* and *Pseudomonas aeruginosa* by establishing a defense mechanism (Pradhan et al., 2013). During a test on mice, the methanolic extract of breadfruit fruit and leaves (500 µg/ml each) was used to treat inflammation by lowering the intensity of leukocyte infiltration by preventing skin tumor growth and angiogenesis induced by carcinogenic chemicals 30 minutes after treatment (Lin et al., 2014). Fruitackin, a lectin isolated from the saline crude extract of breadfruit seed, induced hemagglutination against human and rabbit erythrocytes when added at 0.15 mg/ml and exhibits antifungal activity against *Fusarium moniliforme* and *Aspergilus niger* at the same concentration as used for jackin (2.25 mg/ml, but no effect on *A. niger* at 4.5 mg/ml) (Trindade et al., 2006).

Propagation (classical and biotechnological)

Conventional vegetative propagation using cuttings, grafting and rootstocks have unsuccessfully been used to propagate *A. heterophyllus* and *A. altilis*, thus seed serve as an effective choice to propagate *A. heterophyllus* (Roy et al., 1993). *In vitro* culture is an effective solution to cultivate and mass-produce both species. Roy et al. (1993) first washed adventitious shoot buds in 100 ml of 0.7% polyvinylpyrrolidone (PVP) with 2% sucrose, shook them at 100 rpm for 3 minutes then washed buds with tap water to remove PVP. Buds were disinfected in 0.2% $HgCl_2$ for 5 minutes then rinsed with sterile double-distilled water (SDW) for 3 minutes and this procedure was repeated 3-5 times. Buds cultured on Difco bacto-agar-solidified Murashige & Skoog (1962) (MS) basal medium supplemented with 8.88 µM 6-benzyladenine (BA) and 2.68 µM α-naphthaleneacetic acid (NAA) induced 10 shoots/explant after the 7th subculture. Shoots were elongated on MS medium with 4.44 µM BA, 0.54 µM NAA and 10% (v/v) coconut milk. Shoots were rooted *in vitro* on half-strength MS medium with 5.37 µM NAA and 4.92 µM indole-3-butyric acid (IBA), 80% of shoots being able to root. Plantlets were transplanted into earthen pots containing sterile sand, soil and humus (1:2:1, v/v/v), and 75% survived after 30 days.

Amin & Jaiswal (1993) used 10-20 days' old terminal buds from an *A. heterophyllus* trunk from a 30-50 year-old tree grown from seeds. Stems were washed in running tap water, treated with 1% (v/v) Cevalon® (an antiseptic and detergent), disinfected in 0.1% $HgCl_2$ for 5 minutes, then rinsed with SDW 4-5 times. Explants (5-10 mm denuded buds) were prepared by removing the outer cover of green stipules and excising inner buds encased by creamy-white stipules before implanting them vertically on growth medium, and placing cultures at 26±1°C, a 16-h photoperiod (50-70 µmol m^{-2} s^{-1}), and subculturing them every 4-5 weeks. MS basal medium with four concentrations (4.5, 9.0, 18.0, and 36.0 µM) of BA and kinetin (Kin) and a combination of BA and Kin (4.5 µM each) were used to induce shoots while MS with two concentrations of BA (4.5 µM and 9.0 µM) and BA with Kin (4.5 µM each) were used to multiply shoots. Roots were successfully induced from shoots with four combinations (0.5, 5.0, 10.0, and 25.0 µM) each of NAA and IBA, or two combinations (5.0 + 5.0 and 10.0 + 10.0 µM of NAA and IBA). The highest percentage of bud break resulted from 9.0 µM BA (82 ± 6%) while BA + Kin (4.5 µM each) resulted in 90 ± 7%. The highest number of shoots/explants formed with 4.5 µM BA (3.5±0.6), or 38±1.1 for BA + Kin (4.5 µM each). Under *ex vitro* conditions, the survival percentage of regenerated plantlets was 50%.

A. altilis can be propagated vegetatively *in vivo* and *in vitro*. *In vivo* vegetative propagation can be achieved by cuttings and air layering of branches by removing the ring bark, covering the wound with peat moss and then encapsulating in plastic to induce rooting before being cut and placed on soil (Deivanai & Bhore, 2010), although details about how long it takes to achieve each step was not explained. *In vitro* propagation of *A. altilis* can be achieved using shoot tips (Rouse-Miller & Duncan, 2000; Murch et al., 2008).

Rouse-Miller & Duncan (2000) collected shoot tips from a 6-7 year-old tree during the dry season (December to April in Trinidad-Tobago). Explants with one or two expanded leaves and 3-6 cm of associated stem were collected and placed in water (period of time not specified). Expanded leaves and bracts surrounding the shoot tip were removed and shoots were rinsed in tap water before cleansing in 70% ethanol for 1 minute. Shoots were reduced to 1 cm, dipped in 70% ethanol for 30 seconds, 10% household bleach (5.25% available chlorine) for 10 minutes and rinsed three times in sterile distilled water. The Rouse-Miller & Duncan (2000) study used Margara (1978) nutrients (Table 3).
For shoot induction, N5K and N15K macronutrients (Margara, 1978), MS micronutrients and vitamins with 3% sucrose, 0.8% agar and 4.4 µM BA were necessary. Shoot proliferation required Margara (1978) $N30NH_4$ macronutrients, MS micronutrients, vitamins, 3% sucrose and 2.2 µM zeatin. Rooting required $N30NH_4$ macronutrients, vitamins, 2% sucrose, with 0.5, 1.0, 1.5, 2.0, and 2.5 µM IBA. However, IBA alone could not induce roots, and 60% of shoots formed roots in auxin-free medium ($N3ONH_4$ in Table 3; Margara, 1978). Murch et al. (2008) used MS or B_5 (Gamborg et al., 1968) media with 2.5 g/L gelrite and 3% sucrose, 2 µM BA and 3 µM Kin to induce shoots in *A. altilis* within one week and 1 µM IAA to induce roots.

Table 3. Margara (1978) nutrient lists according to Karla da Silva (2010).

Medium	Macronutrients (mg/L)							
	KNO_3	$NaNO_3$	NH_4NO_3	$Ca(NO_3)_2 \cdot 4H_2O$	$CaCl_2 \cdot 2H_2O$	$MgSO_4 \cdot 7H_2O$	KCl	KH_2PO_4
N5Ca			80	354	292	246	149	136
N30Ca	808		480	1180		246	74.5	136
N30K	1313		480	590		246	74.5	136
N15K*	606		240	354		246	149	136
N15Ca	101		240	944		246	149	136
N45K	1818	85	720	944		246	372.5	136
N5K*	75.8		80	265.5		246	372.5	136
N3ONH$_4$*	606		800	472		246	372.5	136
Medium	**Micronutrients (µg/L)**							
	$MnCl_2$	$ZnSO_4 \cdot H_2O$	H_3BO_3	KI	$CuSO_4 \cdot 5H_2O$	$NaMoO_4 \cdot H_2O$	$FeSO_4 \cdot 7H_2O$	$NaEDTA \cdot 2H_2O$
All	157	500	500	10	100	59	35000	30000

* only the macronutrients were used in the Rouse-Miller and Duncan (2000) study

Molecular advances and future perspectives

Molecular studies of both jackfruit and breadfruit offer promising prospects for exploiting biotechnology- and industry-derived benefits. Breadfruit molecular genetics has been studied more than in jackfruit. Studies on the genetic identification and profiling of breadfruit used microsatellite or short sequence repeats, identifying around 65 loci for nuclear genomic DNA (Witherup et al., 2013; De Bellis et al., 2016) or 15 loci for chloroplast genomic DNA (Elliot et al., 2015). Multi-access identification key software to identify breadfruit cultivars has been developed from a prototype version on a Lucid 3.3 platform based on quantitative and qualitative traits (Jones et al., 2013). Amplified fragment length polymorphism (AFLP) has been used to identify and track the origin of breadfruit cultivars as linked to the routes of human migration in Oceania (Zerega et al., 2004), or to assess genetic diversity (Shyamalamma et al., 2008). Random amplified polymorphic DNA (RAPD) was also used to assess genetic diversity (Prasad et al., 2014) and fruit cracking in jackfruit (Singh et al., 2011). Chloroplast and nuclear DNA were used to assess the phylogeny of 60 Moraceae taxa, including the *Artocarpus* genus (Zerega et al., 2010). Gibberellin 20-oxidase genes isolated from breadfruit allowed for the detection of sequence variants, their role in stem elongation after cuttings were treated with paclobutrazol (a GA inhibitor), and their regulation of abiotic stress, namely salinity and drought (Zhou & Underhill, 2015, 2016). Future research needs to identify breadfruit and jackfruit genetic diversity more precisely while studies on molecular genetics related to metabolic biosynthetic pathways, for example the elucidation of genes coding for artocarpatin synthesis, would allow for applications in the pharmaceutical industry.

Jackfruit and breadfruit are still known locally and may be good sources of nutrients ranging from carbohydrates to secondary metabolites. These fruits could be useful germplasm in future plant breeding projects for improving fruit, such as fortifying stress tolerance. Roy et al. (1993) bred flood-resistance jackfruit plants *in vitro* as a way to solve the problem of annual flooding in Bangladesh. A breeding programme conducted in South Florida aimed to improve jackfruit aroma, edible percentage, flesh firmness, colour and flavour (Campbell et al., 2004). A red-fleshed variant of jackfruit exists in India (International Tropical Fruits Network, 2011). These colour variants can be used to attract more consumers and thus achieve the maximum benefits of jackfruit, thus breeding for more colourful fruit flesh could be important. For the nutraceutical and pharmaceutical industries, future jackfruit breeding for higher content of specific metabolites can be achieved in a similar way as "Gama Melon Parfum," a melon cultivar that was developed in Indonesia to obtain higher yield of sesquiterpenes aimed for perfume production (Maryanto et al., 2014). Breadfruit colouration is mostly only white, but it has some shape variants ranging from oval to long fruits (McCormack, 2007). As breadfruit appears to have potential as a better source of starch used in drug tablets than cornstarch (Adebayo et al., 2006), a breeding programme to produce a higher yield of starch in breadfruit could be a good prospect. Similar prospects for jackfruit could also be applied to breadfruit in future by creating colour variants for increased appeal or to improve metabolite content for the food, pharmaceutical and nutraceutical industries. As one example, breadfruit flour was found to be a good substitute for wheat flour when used as a composite breadfruit-wheat flour mix for donuts, with a larger ratio of breadfruit flour resulting in lighter donuts, apparently as a result if its lower gluten content, although panelists preferred the color, aroma, taste, and texture of donuts with more wheat flour in the dough (Oke et al., 2018).

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