Discover Agriculture

Review

The Tahitian chestnut [*Inocarpus fagifer* (Parkinson ex F.A.Zorn) Fosberg, Fabaceae], a neglected multi-purpose tree from the Asia–Pacific region

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Abstract
The Tahitian (or Polynesian) chestnut *Inocarpus fagifer* is distributed widely in tropical South-East Asia and in the Pacific region. It is an important component in traditional agroforestry systems. However, its importance as a food plant has decreased considerably. There is no evidence that the species has ever been domesticated, nor that deliberate breeding and crop improvement is presently taking place. This article aims to provide an overview of the current status of knowledge about its distribution, biology, its past and current cultivation and use as a species in agroforestry systems, and to analyse its future potential for production, commercial use and plant improvement. *Inocarpus fagifer* grows in lowlands in coastal and near coastal areas, often along rivers. It often forms almost pure stands underneath the canopy trees. *Inocarpus fagifer* trees are very vigorous and shade-tolerant. They thrive in moist to wet soils. Nearly all parts of the tree have been used for multiple purposes including timber, medicine, and animal fodder. The seed has significant traditional importance as human food, and it plays an important role in the diets of rural communities, in particular during the crop harvesting season. *Inocarpus fagifer* is mostly disease-free. Reports about the commercial use of *I. fagifer* remain localised and largely anecdotal. The species retains a good potential for commercial development and for a wider commercial use as an alternative food source. No accessible genebank accessions are available. Fundamental questions on its marketability and genetic potential need to be answered.

Keywords Agroforestry · Cinderella tree · Crop improvement · Ecosystem services · Food security · Canoe plant · Livelihood · Underutilised crop

1 Introduction

Agroforestry systems, which are agricultural systems that integrate trees with crops and/or animals [1], have received increasing scientific attention over the few decades. A growing amount of scientific data published over the last twenty years show that agroforestry systems provide a multitude of different ecosystem services and environmental benefits as well as economic commodities as part of a multifunctional working landscape [2–5]. This is particularly true for traditional agroforestry systems situated in tropical countries, which are important for sustainable agriculture and for food and nutritional security. In tropical Asia and the Asia–Pacific region, agroforestry systems are part of the traditional land use systems [6–8]. They support livelihoods of the rural populations [9] and can serve as an insurance against natural

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disasters [10]. Many indigenous tree species, either planted or protected, have been a part of traditional farming practices for many hundreds of years. Benefits of these trees include timber, food and nutritional security (often particularly used during periods of occasional food shortage), source of income, basis for farming systems protecting the environment, and conserving soils and maintaining biodiversity [11]. However, individual research studies show that as a result of the planting of cash crops and non-indigenous fruits and nuts, e.g. banana, cassava or macadamia nut, traditionally planted or used, local crops for food, medicine and other daily needs are often abandoned, downplayed and no longer actively cultivated [12, 13]. These changes in cultivation are linked to a loss of knowledge about traditional land management and its resources.

The Tahitian (or sometimes called Polynesian) chestnut *Inocarpus fagifer* (Parkinson ex F.A.Zorn) Fosberg (Fabaceae) is a well-known species in the Asia–Pacific region [14] and an important component in traditional agroforestry systems [15]. Pauku [9, 16], in a participatory survey among village communities in the Solomon Islands, showed that villagers considered the species most important as a source of food and income. Given its local and regional significance, it is intriguing to see that Huml et al. [17] called *I. fagifer* an "underutilised legume", and Pauku [9] called it a "Cinderella tree". The term "Cinderella tree" was introduced by Leakey and Newton [18] and is defined as a "traditionally important indigenous species that has been overlooked by science for agroforestry and forestry". There seems to be a conflicting discrepancy between the species' local popularity and its (actual or perceived) importance for agriculture at least in some parts of its area of distribution, and its overall use and promotion in agriculture in the Asia–Pacific region.

The aim of this article is therefore to gather available scientific literature and to provide an overview of the current status of knowledge about *I. fagifer*—what is known about its biology, its past and current cultivation and use across its area of distribution, and its future potential for production and as a species in agroforestry systems in the Asia–Pacific region? Can the results from detailed local studies (such as Pauku [9, 16] from the Solomon Islands and Bourke [12] from Papua New Guinea) be generalised across the species' area of distribution to find general patterns? Can the results from these studies be used in a way to improve propagation and market situation elsewhere? Is plant genetic material readily available for use, e.g., in plant improvement and breeding projects?

2 Taxonomy

Fosberg [19] proposed the name *Inocarpus fagiferus* (Parkinson) Fosberg, and made the combination for Parkinson's previous name *Aniotum fagiferum* Parkinson. The valid name is *Inocarpus fagifer* (Parkinson ex F.A.Zorn) Fosberg. *Inocarpus edulis* J.R.Forst & G.Forst is found in the literature as a widespread synonym. Adema [15] provides the most up-to-date taxonomic reference to *I. fagifer* and compares the species with its congeneric relatives. *Inocarpus fagifer* is one of currently three species in the small papilionoid genus *Inocarpus* belonging to the Fabaceae tribe Dalbergieae. The genus *Inocarpus* is characterized by simple leaves, short inflorescences, a regular corolla, stamens which are adnate to the corolla tube and large orange fruits [15].

3 General habit and morphology

Inocarpus fagifer can vary considerably in growth form and habit. Individuals of the species can be found growing as a straggling bush, as a small, multi-stemmed tree, giving the impression of being coppiced and reaching heights of about 10 m [20], or they can grow into single-stemmed, large trees reaching 20 to even 30 m [21]. I could not find any published information on whether these different growth forms are part of a phenological modification in response to specific habitat conditions or whether they are the result of actual genetic changes that underlie potentially adaptive phenotypic variation. *Inocarpus fagifer* can create dense groves and closed canopies. Already Fosberg [19] described individuals found in some deep valleys of Tahiti which showcase huge buttressed trunks. This observation was confirmed by Huebert and Allan [21], who found mature trees which often form massive buttresses. The tree has a shallow taproot and a well-developed network of lateral roots which appear on the soil surface [22].

The evergreen, dark green leaves of *I. fagifer* are alternate as for the vast majority of species in the Fabaceae family. The leaf blade is 15 to 30 (– 40) cm long and 7 to 13 cm wide (Fig. 1). The leaf base is rounded to cordate. Stipules are 1–2 by 1–2 mm large. The leaf apex is mostly obtuse to rounded, rarely acuminate. The flowers appear usually in November/December and are arranged in clusters. They have a faint sour fragrance. The corolla is 12–15 mm long, with five narrow, yellowish-white petals. The calyx is two-lipped and 5–6 mm long (Fig. 2). Bracts are 0.4–1.5 by 1–2 mm large. The stamens

Fig. 1 Leaves of *Inocarpus fagifer*. French Polynesia, September 2023. Photo: Graham Montgomery, with kind permission

are arranged in two whorls. The style is up to 0.5 mm long. The monocarpellate (one seeded) and indehiscent fruits can be very variable in shape and colour. They are slightly flattened, irregularly ovoid, rounded or oblong [14]. They vary in size, which ranges between 30 and 90 by 45 and 75 by 24 and 40 mm [14, 15]. A single tree produces up to 100 fruits per season, usually between January and May [13]. On islands of Papua New Guinea, fruiting occurs mainly between November and February [12]. The initially green fruits turn orange-brown when ripe [22] (Fig. 3).

Taxonomically and morphologically, the English vernacular name Tahitian (or Polynesian) chestnut is misleading, as the species is not a chestnut (which is a name applied to species in the genus *Castanea*, Fagaceae). Neither is it correct to talk about a nut when describing the fruit, as the pericarp of the fruit is not dry and hard but coriaceous. Using Spjut's terminology [23], the fruit can be classified as a camara. Several authors (for example [13]) refer to the single, kidney-shaped, starchy seed inside the fruit as a "kernel". The word "kernel", colloquially defined as "the inner softer part of a seed, fruit stone, or nut" is not a scientific term and should be avoided all together. In this paper, I therefore simply talk about a "seed". It has a size of 5 × 7 cm. The tree bark is rough and brown or grey [22].

4 Origin and distribution

Inocarpus fagifer is distributed widely in tropical South-East Asia and in the Pacific region, in particular in lowlands from sea level to 400–500 m a.s.l. altitude in coastal and near coastal areas (Fig. 4). With a long history of ancient introductions across large parts of Oceania [24], the identification of its original native area of distribution in Malesia and the exact pathways of its subsequent anthropogenic dispersal to Near and Remote Oceania eastwards to the Marquesas Islands of French Polynesia [21] in pre-historic times remain unanswered questions. As Adema [15] put it, the natural distribution of *I. fagifer* is obscured by the long history of human dispersal as a cultivated species. Whistler [25] listed the species as one of the important canoe plants that the first Polynesian settlers took with them on their seafaring journeys eastwards colonising vast parts of the Pacific Ocean, something that had already been suggested by Corner [20]. This notion is supported by archaeological evidence presented by Kirch [26] who could show *I. fagifer* as being among other economically important plants during the colonisation by Polynesian settlers.

Inocarpus fagifer is common in the Indonesian province of Maluku, the islands of Borneo, Sulawesi and New Guinea [12], in parts of the Philippines but it is rare in Java. Authors disagree whether the somehow isolated populations in east

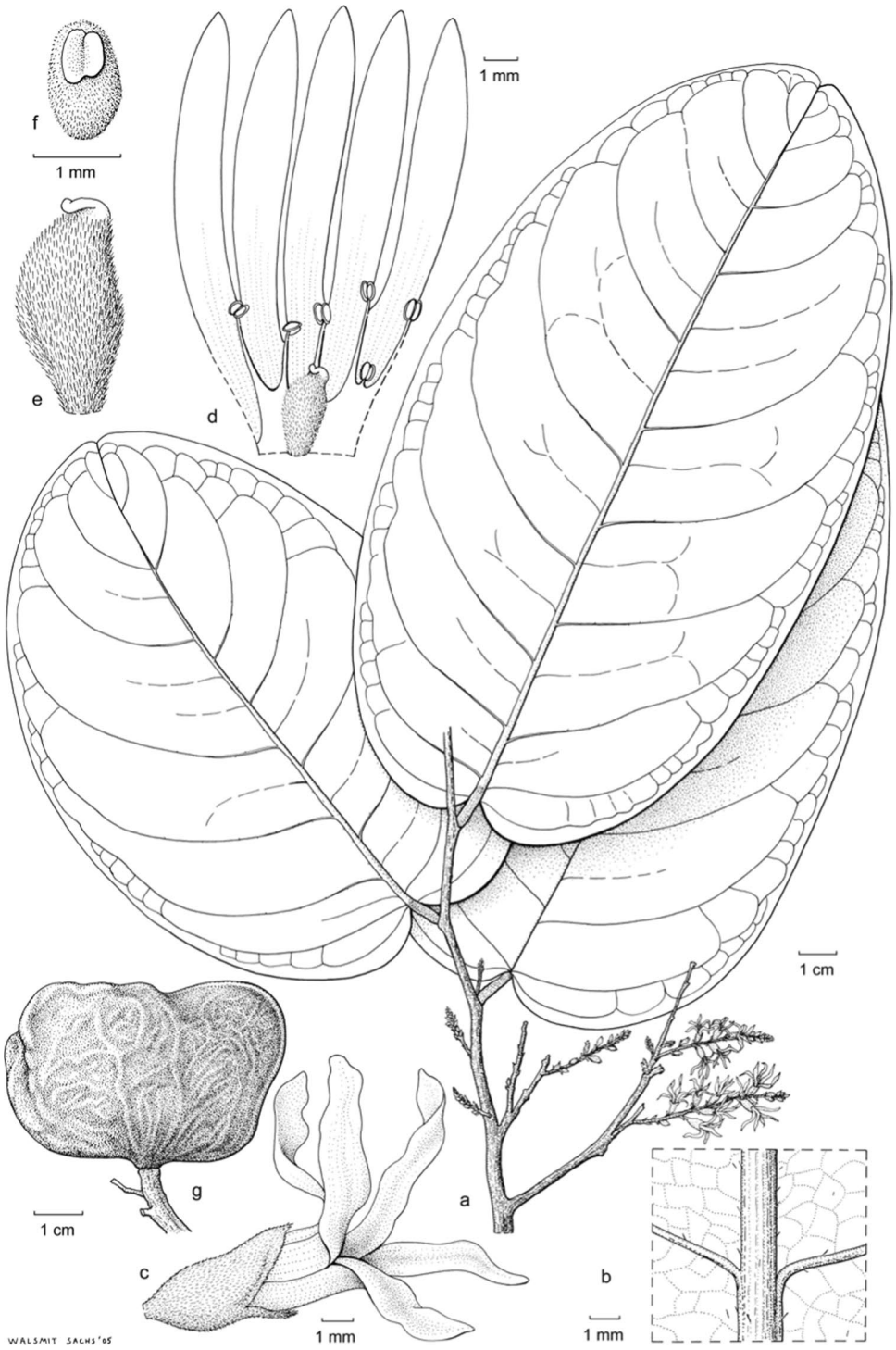

Fig. 2 *Inocarpus fagifer*, **a** Habit; **b** detail of lower surface of leaf; **c** flower; **d** corolla from inside; **e** pistil; **f** stigma from above; **g** pod. Artist: Anita Walsmit Sachs, reproduced from [15] and shown here with kind permission under a CC BY-NC-ND license

Johor in Peninsula Malaysia are natural or man-made. Corner [20] was convinced that those populations are wild and natural components of tidal forests, whereas Walter and Sam [14] and Thomson et al. [24] spoke about human introductions. The species is distributed (most likely naturalised after ancient introductions) in Micronesia (Kiribati, Marshall Islands and certain islands of the Federated States of Micronesia). It occurs widely in Melanesia (Papua New Guinea including the Bismarck archipelago [12], the Solomon Islands [9, 16, 27], Vanuatu, and Fiji). It is rare in New Caledonia [28]. In Polynesia, the species is distributed widely in Tonga, Samoa, the Cook Islands and French Polynesia. The dubiousness among scientists about the naturalness (or not) of populations of *I. fagifer* in Polynesia becomes evident when for example Pauku [9, p. 128] mentioned that the species occurs as an indigenous species to many Polynesian countries, only to continue

Fig. 3 Ripening fruits of *Inocarpus fagifer*. Vanuatu, September 2015. Photo: Dominik M. Ramík, with kind permission

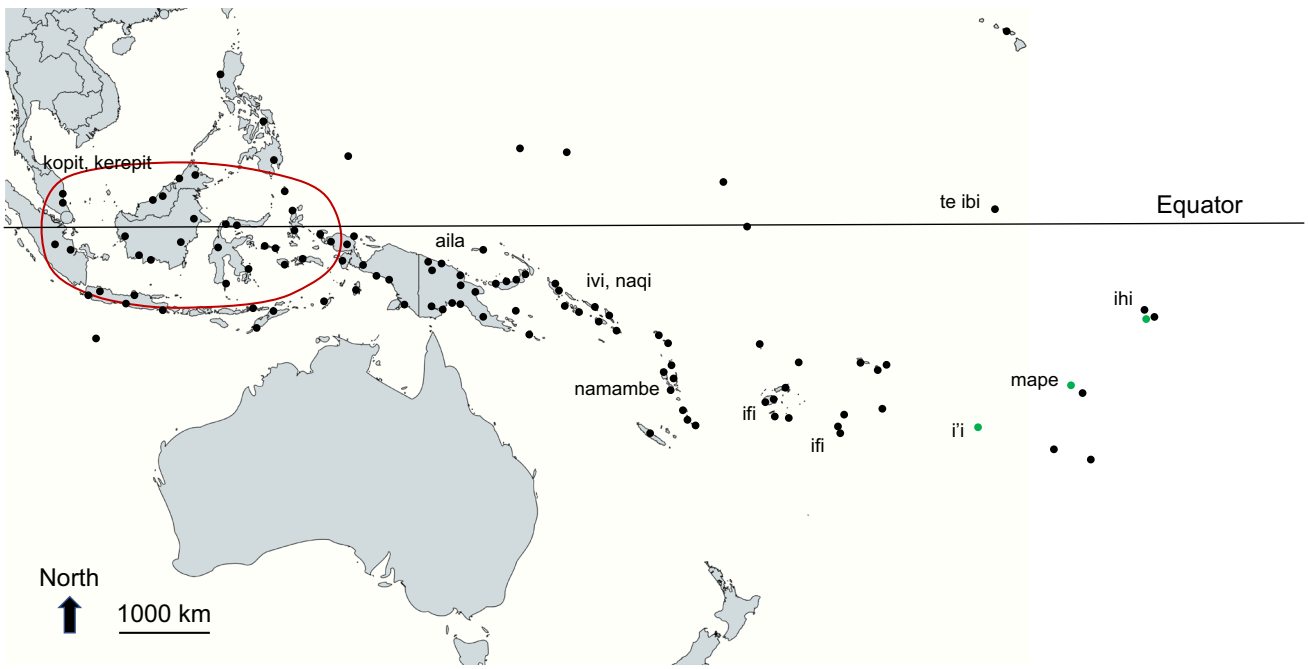

Fig. 4 Map showing the current area of distribution of *Inocarpus fagifer* in South-East Asia and in the Pacific region, with examples of local vernacular names provided. The red ellipse indicates the presumed original native range in Malesia. Black dots show its current (native and introduced) occurrence across the region. Green dots show localities of archaeological finds before European arrival, as mentioned in the text

that the species was believed to be an aboriginal introduction in parts of Polynesia and Micronesia. Evans [13] confirmed its native status in Vanuatu. Harrison and Karim [29] reported it as a common wild species in Fiji—already Seemann [30] had referred to the species as one of the most common trees in Fiji.

For most of the Pacific islands, precise times of the human-facilitated arrival of *I. fagifer* are difficult to identify, due to the lack of genetic, palaeobotanical and archaeological data. Archaeobotanical evidence from Maupiti (Society Islands, French Polynesia) presented by Dotte-Sarout and Kahn [31] shows that *I. fagifer* appeared late in Eastern Polynesia, and reached the Marquesas Islands by 1650, if not earlier. Outside the South-East Asian and Pacific regions, the species was introduced into Hawai'i (USA) in more recent times [15, 24] and to some parts of the Caribbean.

Huebert and Allan [21], studying anthropogenic forest changes in the Marquesas Islands found that such changes taking place at low and mid altitudes extensively remodelled the natural vegetation in pre-historic times. Polynesian settlers established productive and diverse arboricultural gardens, in which *I. fagifer* was an important tree. By 1650 CE, the low- and mid-elevation vegetation was extensively remodelled. Breadfruit (*Artocarpus altilis* (Parkinson) Fosberg), *Inocarpus fagifer* and other economic species became widely established and cultivated. Dotte-Sarout and Kahn [31] showed for the French Polynesian island of Maupiti that the species was an essential crop in low-lying areas as early as the seventeenth century. Despite the lack of ethnographic descriptions of specific traditional subsistence practices at or before European contact, one can comfortably assume that *I. fagifer* was firmly incorporated in the cultural and economic systems of the arriving Polynesian colonizers. Further work would be needed to investigate how *I. fagifer* and other crop trees, whether introduced or indigenous on specific islands in South-East Asia and the Pacific region, could have been at the foundation of a cultural landscape that colonists actively modelled in the few centuries following their arrivals [31]. Multiple vernacular names exist for *I. fagifer* across its area of distribution, some of which are included in Fig. 4.

5 Ecology

In many places, *I. fagifer* forms almost pure stands as the most common understorey tree underneath the dominant forest canopy trees. *Inocarpus fagifer* trees are very vigorous and shade-tolerant. They thrive in moist to wet soils, and although their roots are often immersed almost continuously in water, the species does not appear to have pneumatophores. Corner [20] found that it is very common in the mildly brackish, tidal swampy forests in parts of east Johor (Peninsula Malaysia) from near the sea to some ten miles inland. In Java, individual trees can be found along river banks and canals, growing in moist soil [32]. Walter and Sam [28] reported that *I. fagifer* is often seen in villages and village gardens. It can be assumed with a high degree of certainty that in many cases, the species will have escaped from cultivation and colonised natural or secondary forests (Fig. 5).

6 Uses of the species

6.1 Seed

While nearly all parts of the tree have been used for multiple purposes by various cultures in the Asia–Pacific region, the seed has significant traditional importance as food, and it plays an important role in the diets of rural communities throughout the species' area of distribution, in particular during the crop harvesting season [12, 13]. Huml et al. [17] even called the seed a "traditional staple food of the Pacific region". At the same time, the seed may constitute a food supply insurance during times of natural disasters, when imported food and commercial crops are temporarily not available [10]. Kinaston et al. [33] referred to nuts and fruits of other crop trees as snacks which in the Solomon Islands are traditionally eaten outside the main meal. Although these authors did not explicitly mention *I. fagifer*, it can be assumed that its seeds, consumed as part of a main meal or outside mealtimes, were an important source of calories and nutrients. Pollock [34] called snacks outside main mealtimes "non-meal edibles". In Tahiti and possibly elsewhere, non-meal edibles are part of complex dishes, which are cooked packed in an earth oven.

The fruits, containing the seeds, are harvested either directly from the tree at maturity or they are collected after they have fallen to the ground [9]. Pauku [16] states a yield of up to 75 kg fruits per tree and year for individual trees older than 25 years. The seeds are then extracted from the fruits. The seeds must be cooked (usually roasted in hot ashes or boiled) before consumption to remove mild toxins [14, 35]. Alternatively, the entire fruit can be baked, and the seeds extracted afterwards [36]. The taste is described as rather bland [13]. Seeds are also stored in underground pits after

Fig. 5 Specimen of *Inocarpus fagifer* in a forest setting. Cook Islands, April 2022. Photo: Jon Sullivan, with kind permission (CC-BY licence)

partial fermentation, as it is done with breadfruit [28]. The seeds can also be processed into a sort of jam [13]. In contrast, the seed testa and other parts of the fruit are not edible.

Handy [37, 200] provided the recipe of a popular dish *piahi* in the Marquesas Islands, prepared from grated *I. fagifer* seed mixed with coconut milk and baked in a stone oven.

*The ihi nut (*Inocarpus edulis*), which may be roasted and eaten in the same way as the chestnut of America, is delicious when made into a piahi* [= anything grated and mixed with coconut milk, and baked in a loaf]. *The nut is cut open with an axe (formerly, the natives say, there grew an ihi which could be bitten open or torn apart with the fingers), the kernel is removed and soaked overnight, so that the dark skin can be peeled off. The kernel is then grated* […] *into the coconut milk, the immediate immersion in the liquid preventing it from turning dark and rancid. The milk and gratings are stirred constantly until a thick batter is formed. This is wrapped in banana leaves in long, flat packages, and baked in the oven.*

I am aware of only two studies which looked at the nutrient content of the seeds. Setyowati and Wawo [38] analysed seeds from populations in west Java and found a high content of carbohydrates (75.79 to 77.70%). Huml et al. [17] analysed *I. fagifer* seeds for the presence of fatty acids, minerals, phenolic compounds (ferulic and coumaric acids being the most abundant phenolics) and B vitamins. Within the oil fraction, 14 unsaturated fatty acids and 21 saturated fatty acids were detected. The overall profile demonstrated a greater portion of polyunsaturated fatty acids (31%) over monounsaturated fatty acids (22%). The results of a mineral elements analysis showed that calcium, potassium, magnesium, phosphorus and sulphur were the most abundant elements, with a significance presence of micronutrients such as Cu, Mg, Mn and Zn. Huml et al. [17] concluded that seeds constitute a valuable dietary source.

6.2 Timber

Although Walter and Sam [28] stated that the wood of *I. fagifer* was of little use, other authors reported on a multitude of different uses. The use of the wood as firewood is often mentioned [for example, 9, 25, 31, 39]. Handy [37] and Huebert and Allan [21] reported on the use of large branches as firewood for a traditional earth oven *feikai mei* in the Marquesas

Islands. In addition, the wood is used for light constructions, for tools such as axe handles, spears, and tapa cloth beaters [24], but also for furniture making (bed frames) and canoe manufacturing [9, 16, 25].

6.3 Medicine

While it is not uncommon at all to find literature references to the medicinal use of parts of the tree, these references seem to be based more on anecdotal evidence than pharmacological and ethnopharmacolocial research studies, and they lack any required detail to withstand scientific scrutiny. In Borneo and Java, tannin from the bark is taken internally as a remedy against intestinal disorders, which is consistent with Walter and Sam [28] and Pauku [16] who reported on the use of the bark to treat urinary infections. In the Marquesas Islands, the bark has medicinal uses [21], and Huml et al. [17] stated in rather general terms that various parts of the tree are used for medicinal purposes. The juice from the mesocarp of green fruits is used in Tonga to treat insect bites and burns [40].

6.4 Animal fodder

The leaves of *I. fagifer* are used as animal fodder [24, 32, 39]. Seeds are valued to feed free-range chicken [16, 24, 40].

7 Role of the species in the forest ecosystem

In addition to the various direct human uses of various parts of *I. fagifer* as summarised above, the species plays an important role in the forest ecosystems throughout its area of distribution, and provides additional ecosystem services to the local populations.

In Samoa, *I. fagifer* fruits are regularly eaten by different species of fruits bats in the Pteropodidae family, in particular during February and March when the availability of other fruits is limited [41]. A recent survey conducted in the Philippines shows that four different species of fruit bats regularly visit *I. fagifer* forests in the Philippines, that might act as pollinators for the tree while feeding on the nectar [42]. Fruit bats also contribute to the dispersal of the tree [28, 42]. The tree is a food source for birds and provides nesting site [29]. The extensive network of lateral roots extends a long distance from the trunk, which is useful for erosion protection and for the stabilisation of coastal land [16].

8 Past and current cultivation

Inocarpus fagifer is an important element in traditional agroforestry systems in the Asia–Pacific region. In islands of the Bismarck Archipelago and in the islands of Milne Bay Province (Papua New Guinea), the species is an important element of traditional village agriculture [12]. Pauku [9] showed for the island of Kolombangara (Solomon Islands) that *I. fagifer* trees grow naturally in old gardens and in different types of forests. In Vanuatu, individual village communities recognise an average of six (but up to 18) different cultivars which all carry specific names, in addition to many unnamed cultivars with highly variable fruits [14]. Pauku [16] and Thomson et al. [24] observed significant intraspecific variation in leaf and fruit shape and colour, with farmer-selected cultivars recognised not only in Vanuatu but also in Samoa and Tonga. Farmers in Solomon Islands confirmed that they select for trees with desirable seed characters [9]. Despite these reports on existing cultivars and the fruit variability, there is no evidence that *I. fagifer* has ever been domesticated [43], nor that deliberate breeding and crop improvement is taking place.

As part of traditional agroforestry systems, *I. fagifer* acts as a shelter and shade tree, in particular for crops such as taro (*Colocasia esculenta* (L.) Schott) and giant taro (*Alocasia macrorrhizos* (L.) G.Don) [9, 29, 40]. Harrison and Karim [29] gave the example of a coastal site near Nadi in western Viti Levu (Fiji), where taro was planted as a farm household food crop next to an *I. fagifer* tree. Providing shade, wind protection, and avoiding topsoil drying are important during the establishment of the young taro plants. However, according to Pauku [16], *I. fagifer* should not be planted right next to taro and other light-demanding agricultural crops because of its dense canopy and suggests that only shade-tolerant agricultural crops should be planted in its vicinity.

Throughout the Pacific region, the importance of *I. fagifer* as a food plant has decreased considerably, and increasingly so over the last 60–70 years [36]. Walter and Sam [14] pointed out that its cultivation in the region has declined, although no official production statistics are available to quantify this decline, which is seen as the result of the widespread

adoption of cassava and the increase of cultivation of sweet potato in rural agricultural systems [12] and of the availability of imported rice as an alternative food source [16]. Lepofsky [44] showed that the cultivation practices of the Maohi in the Society Islands of French Polynesia have undergone considerable changes since the time of European contact. Today only a limited number of traditional and introduced crops are raised in family gardens and fields. Of the traditional food plants, banana, taro, breadfruit, sweet potato, and yams are still commonly eaten, but many other previously widely cultivated plant species are no longer cultivated. Labour-intensive methods, such as nursery gardens or terraced irrigated fields, are no longer practiced [44]. In Papua New Guinea, the seeds of *I. fagifer* are not popular outside the immediate areas where *I. fagifer* trees grow [12]. Current cultivation of *I. fagifer* in the French Polynesian Society Islands could not be confirmed [44], despite the fact that villagers are eating the seeds.

Naturally germinated seedlings are plentiful but are usually not allowed to grow in order to keep the area clear around adult trees so to ease the gathering of the fruits. Although *I. fagifer* can be easily propagated by single-leaf stem cuttings or by planting seeds, and detailed propagation protocols are published [16], active new planting happens, if at all, only on a small scale. This is done either by planting a mature fruit or by transplanting a young seedling, Already Corner [20] pointed out that the Malays did not make any efforts to cultivate *I. fagifer*. There are no published data available on propagation and active planting of the species, so it is not possible to estimate or calculate the scale of propagation and planting. No information about specific pre-planting measures is known [16].

9 Pest and diseases

Inocarpus fagifer tends to be mostly disease-free; only few literature references mention pest and diseases. Pauku [16] observed very moderate infestations of young leaves by leaf miners in the Solomon Islands. No major pests or diseases are known to attack mature foliage. Developing flowers and fruits are susceptible to fruit flies, whereby the fruit flies lay eggs on the skins of the immature fruits, and the hatched larvae burrow themselves into the fleshy mesocarp [9]. Severe fruit-fly infestations may result in a total loss of yield, although some cultivars appear more resistant to fruit-fly attacks than others [24].

10 Commercial use

While the importance of *I. fagifer* as a food plant has decreased considerably over the last 60–70 years as mentioned above, there are no data or statistics available to quantify this decline, neither there are data available regarding its production and commercial use. Such data would be essential to answer the question to which degree *I. fagifer* is a commercially under-used and neglected crop. Reports about the commercial use of *I. fagifer* remain localised and largely anecdotal. In the Solomon Islands, surplus stock is commonly traded at local food markets [9]. Although local people in Java are generally not familiar with the tree or with its actual or potential utilisation, seeds are processed into a snack and sold in Jakarta on a limited scale [38], whereas Bourke and Harwood [36] reported for parts of Papua New Guinea that the seeds "can be found in local farmers markets". Bourke and Harwood [36], in their most detailed overview over agriculture in Papua New Guinea, did not give any production figures for *I. fagifer*. Overall and until up-to-date statistics become available, it has to be assumed that commercial use including commercial marketing of *I. fagifer* does not take place beyond a rather limited, local scale [13].

This assumption stands in stark contrast to the potential of *I. fagifer* for commercial development and for a wider commercial use as an alternative food source [12, 38], not at least because of the nutritional value of the seeds and the general disease resistance of the tree. Before this potential can be fulfilled and the actual prospect for commercial development and use be changed to higher levels, fundamental questions need to be answered—currently limited or entirely unavailable information on various aspects of *I. fagifer* is at the moment one of the main obstacles.

For example, there is contradictory information about the storability of the seeds. While according to Evans [13], the seeds are easily stored and transported, which would make them good candidates for commercial marketing, Pauku [9] found that the fresh seeds possess only a limited shelf-life and deteriorate quickly, which would limit their commercial prospects at least until appropriate preservative methods are found. Air drying and smoking are two locally applied preservation methods. In Vanuatu, fresh fruits are dried on bamboo racks and in the dark, and thus stored for several months, whereas in Fiji, the fruits are smoked to extend the storability of the seeds [16]. Walter and Sam [28] reported on an effective traditional preservation technique, which consists of burying the seeds in a deep pit, or keeping them

flat between two layers of grass. However, there are no quantitative data available on such preservation techniques or storage improvement more generally, and major postharvest handling challenges remain [24].

11 Availability in gene bank collections and current breeding work

Ex-situ gene bank accessions of *I. fagifer* are not available. An online search on global databases for plant genetic resources (Genesys PGR [45], FAO WIEWS [46], GRIN Global of the U.S. National Plant Germplasm System [47], and the seed list of the Royal Botanic Gardens Kew's Millennium Seed Bank [48]) showed that no active, accessible gene bank collection exists at all, anywhere in the world. NPGS [47] lists seven historic collections in their database, of which four accessions were sampled in French Polynesia, and one accession from Honduras, the youngest accession dating from 1981. Genesys PGR [45] lists one doubtful accession from Honduras dating from 1946, stored at CATIE, Tropical Agricultural Research and Higher Education Centre Costa Rica. The apparent lack of accessible gene bank accessions of *I. fagifer* does not necessarily mean that no accessions exist. It might be possible that hidden accessions exist in a gene bank, but that their passport data have not been registered or shared with the global databases. But if this were the case and such accessions existed, as information about them are not available, they would remain hidden and inaccessible for researchers and breeders. To the best of my knowledge, no breeding work is happening.

12 Future directions

Inocarpus fagifer has been traditionally used in agroforestry systems in the Asia–Pacific region, and although this use has declined, the tree is still used locally and perceived as a valuable multipurpose tree by local village communities over large areas of the Pacific Ocean. It is currently impossible to quantify its present underuse. Nevertheless, the species retains a great potential for commercialisation and income generation for those village communities and as a component in a sustainable agroforestry production systems [8, 9]. Thomson et al. [24] recognised the scope for a range-wide selection and breeding programme to improve commercial traits in this species, especially seed size and value improvement as human food. One has to critically ask whether a breeding programme should be implemented for *I. fagifer* at all. A breeding programme with the aim to introduce a new commercial crop to be cultivated in monoculture would be culturally out of context and would contravene the species' appearance in traditional agroforestry systems that pre-dates the European arrival in the Pacific region. Any new breeding should be kept in line with such traditional systems. In any case, in order to be used on a wider scale and commercially, several questions on various aspects need to be answered. First of all, additional knowledge on its local and traditional uses should be gathered. Secondly, a standard characterisation and inventory project including genetic and chemical features should map existing local varieties across its entire area of distribution. The diversity of local varieties on specific islands could indirectly pinpoint towards possible areas of origin and diversification and could help reconstruct the dispersal history across the Pacific Ocean. With this information, studies on its use and marketability could be conducted [11]. Standard techniques for the removal of the toxins present need to be developed. Some cultivars are said to have less toxicity, but this needs to be tested. If it is true, low toxin cultivars will need to be propagated and distributed. Regardless of processing techniques, it seems likely the flavour of the rather bland taste of the seeds needs to be improved [35]. Thomson et al. [24] wanted to see the species used as a major component of multispecies agroforestry and reforestation programs in low-lying coastal areas. Harrison and Karim [29] considered *I. fagifer* an ideal urban species, providing urban beautification and shade for parks and streets. Traditional farming systems of the Asia–Pacific region are inherently resilient. Climate-smart agriculture, using traditional multicrop garden systems is an approach being recommended to achieve sustainable agricultural development for food security under climate change [49]. *Inocarpus fagifer* might play a significant role in this.

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Declarations

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