A critical review of Pongamia pinnata multiple applications: from land remediation and carbon sequestration to socioeconomic benefits

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Review

A critical review of Pongamia pinnata multiple applications: From land remediation and carbon sequestration to socioeconomic benefits

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ABSTRACT

Pongamia pinnata (L.) Pierre (Pongamia) is a tree native to Southeast Asia. Recently, interest in Pongamia focused on its potential as a biofuel source as its seeds contain around 40% oil. However, Pongamia has multiple applications beyond biofuel production. It is a legume, can form symbiotic associations with mycorrhizal fungi, has been shown to be tolerant to drought, salinity, and heavy metals in soil, and has potential to mitigate climate change. Additionally, Pongamia oil has medicinal properties, can be used as biopesticide, insect repellent, to produce soap, and as a source of edible grade vegetable oil. The seed cake can be used as a source of bioenergy, food and feed protein, and organic fertiliser, and the flowers are a good source of pollen and nectar. Pongamia can also bring socio-economic benefits as its ability to restore degraded and contaminated land provides opportunities for local communities through novel valorisation pathways. These multiple applications have potential to form part of a circular bioeconomy in line with sustainable development goals. Although research on the multiple applications of Pongamia has grown considerably, knowledge gaps remain and these need to be addressed so that the full potential of Pongamia can be achieved. Further understanding of the mechanisms underlying its resilience to abiotic stresses, phytoremediation potential and biotic interactions should be a priority, and co-ordinated breeding efforts will be key. Here, we critically review the available literature on Pongamia and highlight gaps in knowledge in which future research should focus on to ensure that the full potential of this versatile tree can be achieved. We conclude that Pongamia can potentially form part of a circular bioeconomy and that harnessing the multiple applications of Pongamia in a holistic manner, with collaboration among key stakeholders, is crucial for the successful application of its benefits far beyond biofuel production.

1. Introduction

Pongamia pinnata (L.) Pierre (Pongamia) is a tree which traditionally, has been used in India and neighbouring countries as a source of traditional medicines, green manure, wood, animal fodder, fuel, biopesticide, and fish poison (Islam et al., 2021). More recently, interest in Pongamia focused on its potential as a biofuel source as its seeds contain around 40% oil. It is also able to tolerate a broad range of climatic and edaphic conditions so it can be cultivated in marginal land (Kesari et al., 2013), thereby reducing competition for land with edible crops. Its ability to fix nitrogen symbiotically poses a significant advantage as, except for soybean, all first-generation biofuel sources are non-legumes (Kazakoff et al., 2010). This considerably increases the suitability of Pongamia as a biofuel source since it can potentially reduce the need for synthetic nitrogen fertiliser (Gresshoff et al., 2015). Pongamia is a member of the Papilionoidea sub-family of *Fabaceae* (*Leguminosae*) family which is characterised by the ability to fix nitrogen symbiotically (Kesari et al., 2013). It is synonymous to *Millettia pinnata* (L.) Panigrahi and both names are commonly found in the literature as (Geesink, 1984) combined both genera without creating a new combination at species level for *P. pinnata*. A list of synonyms and common names is provided in Table 1.

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Table 1
List of synonyms and common names of *Pongamia pinnata* (L.) Pierre adapted from: Csurhes and Hankamer (2016)

Synonyms	*Cajum pinnatum* (L.) Kuntze,
	Cytisus pinnatus L.
	Dalbergia arborea Willd.,
	Derris indica (Lam.) Benn.
	Galedupa indica Lam.
	Galedupa pinnata (L.) Taub
	Galedupa pungum J.G. Gmel.
	Millettia novo-guineensis Kaneh. & Hatus
	Millettia pinnata (L.) Panigrahi
	Pongamia glabra Vent. (nom. Illeg.)
	Pongamia mitis (L.) Kurz
	Pongamia xerocarpa Hassk.
	Pterocarpus flavus Lour.
	Robinia mitis L.
Common names	**Arabic:** Uum al shuur
	Burmese: Thiuwia
	Cantonese: Honge tree
	Chinese (pinyin): Shui huang pi
	English: Indian beech, karum tree, mullikulam tree, pongam, pongam oil tree, poonga-oil-tree, seashore mempari
	Filipino: Báni
	French: Arbre de pongolote
	Hindi (Bengali, Sanskrit): Kanji, Karanj, karanja, Naktamala
	Indonesian: Bangkong, biansu, ki pahang laut, kranji, melapari, Thinwin
	Lao: Dok kom koi
	Malay: Biansu, kacang kayu laut, malapari, mempari, pari- pari, pongu
	Nepali: Karauini
	Singhala: Galkaranda, kona, magulkaranda
	Sinhala: Karanda
	Tamil: Coqueluche, dalkaramcha, pongam, poona, pungai, pungam, punka, punku
	Thai: Kerong, khayi, ko:m ko:y, yinam, vesi ne wai, vesivesi
	Urdu: Suckh chain

Pongamia presents wide genetic variability which can result in high variability in terms of yield. Therefore, a lot of work to date has focused on the identification of 'elite varieties' with superior economic yields and agronomic traits, as well as on the development of propagation methods, and management techniques (Mukta and Sreevalli, 2010). The phytoremediation potential of Pongamia is also being explored (Prasad, 2019), and the use of crops with high bioenergy potential for the phytoremediation of contaminated soils can potentially provide both socio-economic and ecological benefits. Agroforestry is another area where Pongamia can potentially provide benefits. Its flowers provide a good source of pollen and nectar for bees (Raju and Rao, 2006), and the honey produced could increase profitability (Daisy et al., 2001). Furthermore, its extensive network of lateral roots is known for controlling erosion and, due to its large tap roots, it can potentially reduce competition for water with other crops (Leksono et al., 2021) as Pongamia is able to remove water from deeper soil layers than other biofuel candidate trees as its tap roots can extend up to 10m down the soil profile (Garg et al., 2014). It can also be part of climate change mitigation strategies as it has a high carbon sequestration potential (Prasad, 2021), and be an alternative source of protein and vegetable oil as Terviva®, an American based agricultural technology company, has patented methodologies to use Pongamia as a source of plant protein for human and animal consumption and to refine its crude oil into food-grade vegetable oil. They also claim that the production can be carbon-negative which can have a huge impact on food-security in the future (Terviva, 2020).

Here we aimed to identify the most significant literature on Pongamia, both from scientific databases and grey literature, and critically evaluate it based on its contribution to the different areas covered, from its natural history, ecology, physiology, and genetics to its potential as a source of sustainable biodiesel, food, and as a phytoremediation tool. We also aimed to identify gaps in knowledge in which future research should focus on to ensure that the full potential of this versatile tree can be achieved. We have also made a set of recommendations based on our finding that Pongamia has the potential to be part of a circular bioeconomy if optimal valorisation of its multiple applications can be achieved. In a circular bioeconomy, biomass is used in integrated, multi-output production chains (e.g., biorefineries) in an energy-efficient way while making use of residues and wastes and maximizing its value over time in cascading processes (Stegmann et al., 2020). In the case of biodiesel, it is argued that only when its by-products are converted into value-added products, it will be economically viable (Mitra et al., 2021).

An up to date, comprehensive, and critical review on the multiple applications of Pongamia is lacking and our aim is for our study to act as a source of valuable information for stakeholders interested in Pongamia and as a starting point for further evaluation, both in terms of informing future research based on knowledge gaps, but also by changing the status-quo and exploring the place Pongamia may have in a circular bioeconomy.

1.1. *Native range and distribution*

Pongamia is considered to be indigenous to the Indian subcontinent and Southeast Asia, and is reported to be present in Australia, Bangladesh, Brunei, Caribbean, China, Djibouti, Egypt, Fiji, India, Indonesia, Japan, Kenya, Malaysia, Mauritius, Myanmar, Nepal, New Zealand, Nicaragua, Northern Marianas, Pakistan, Papua New Guinea, Philippines, Samoa, Saudi Arabia, South Africa, Seychelles, Singapore, Solomon Islands, Sri Lanka, Sudan, Taiwan, Tanzania, Thailand, Tonga, Uganda, United States, Vietnam, Zambia, and Zimbabwe (Fig. 1) (CABI, n.d.; Csurhes and Hankamer, 2016; Orwa et al., 2009). However, given Pongamia's long history of cultivation and transportation, which goes back to at least the 19th century, it is difficult to establish whether the species is native or naturalised. In Australia for example, some sources consider Pongamia to be naturalised (Orwa et al., 2009), while others consider it to be native (Csurhes and Hankamer, 2016), which is supported by reports that it was used as fish poison, as a source of timber, and as seasonal cue by the aboriginal people (Bottoms, 2000; Thomson, 1936). It was introduced to the United States, first in Hawaii in the 1860's and later to the mainland in the beginning of the 20th Century by the seeds obtained from India, Sri Lanka, Mauritius and Egypt. Risk assessment reports done in both Australia and Zambia concluded that there is no evidence of Pongamia exhibiting invasive behaviour (Csurhes and Hankamer, 2016; Warr, 2013), likely for following reasons: (i) seeds require warm and wet conditions, (ii) germination viability decreases within one year precooling seed bank establishment (iii) it has only moderate and non-invasive formation of suckers, (iv) the unpalatable seeds are not attractive to foraging animals (Kazakoff et al., 2010).

1.2. *Ecology and botanical characteristics*

Pongamia is considered to be a maritime species as it grows naturally along riverbanks and coastal regions with its roots in fresh or salt water. It thrives in humid tropical and subtropical climates but can tolerate a wide range of climatic conditions, from light frost to up to 50 °C and between 500 and 2500 mm mean annual rainfall, requires a dry season of two to six months, and grow in altitudes up to 1200 m (Islam et al., 2021). It can grow on a broad range of soil types including rocky, heavy clay, sandy, alkaline, and saline soils (Usharani et al., 2019), however, it performs best in well drained sandy-loam soil with adequate moisture. It can also tolerate shade as well as full overhead light but performs poorly when grown on soils with pH > 7.5 (Csurhes and Hankamer, 2016; Dwivedi et al., 2011; Orwa et al., 2009).

In terms of its botanical characteristics, Pongamia is an evergreen or briefly deciduous tree which can grow up to 25 m high. It has alternate hairless trifoliate leaves which are light red when young and turn glossy dark green when mature (Fig. 2a). Inflorescences are 6–27 cm long with 2–4 pairs of fascicled flowers with white to pink corolla (Fig. 2b). The

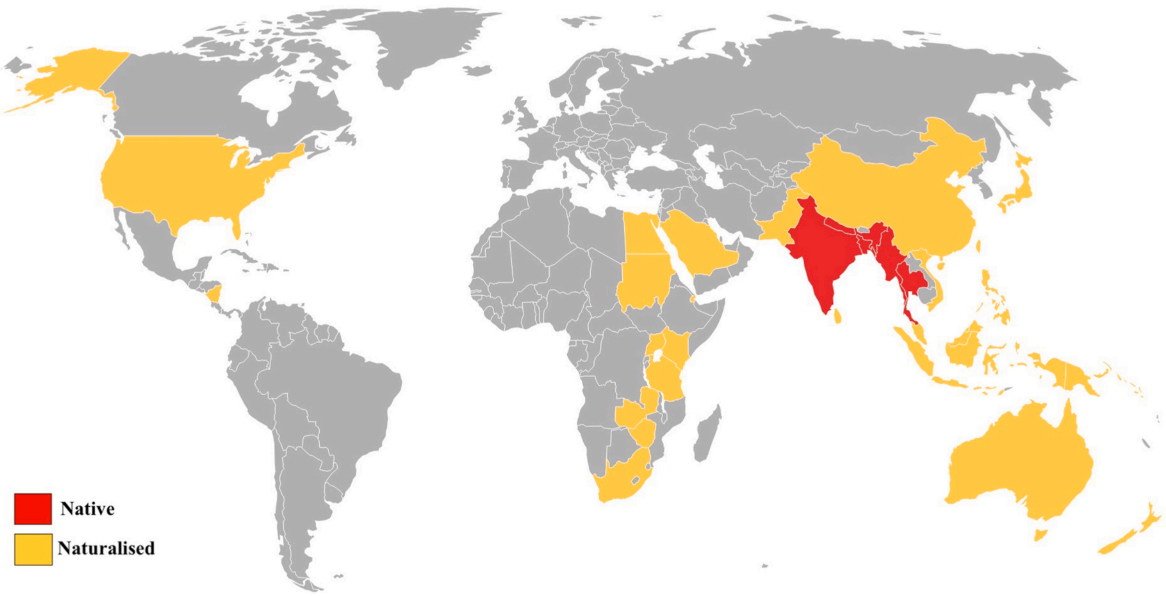

Fig. 1. Global distribution of *Pongamia pinnata* showing Pongamia's native Southeast Asian origins and naturalised land areas where it is present today.

Fig. 2. Pongamia: **a)** Mature Pongamia tree; **b)** Pongamia inflorescence which are 6–27 cm long with 2–4 pairs of fascicled flowers with white to pink corolla; **c)** Pongamia pods containing 1 to 2 flat, dark brown, elliptical, or bean-like seeds; **d)** Mature Pongamia seeds containing around 40% oil. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

ovary is short-stalked and pubescent generally containing two, and exceptionally, three ovules. Pods contain one to two flat, dark brown, elliptical, or bean-like seeds (Fig. 2c and d). It has a large network of lateral roots with a tap root which can extend up to 10 m into the soil profile (Islam et al., 2021). Detailed description of botanical characteristics have been reported (Islam et al., 2021; Orwa et al., 2009).

2. Plant physiology

2.1. Abiotic stresses: Salinity and drought tolerances

Studies evaluating Pongamia tolerance to salt stress, go back a long way and initially were mainly carried out in India by measuring plant morphological and biochemical responses under exposure to a range of salinity levels. Soils are considered to be saline when their EC is higher than 4 dSm^{-1} and water exceeding 4.7 dSm^{-1} is generally not suitable for the irrigation of most crops (Myers et al., 1995). In both pot and field trials, Pongamia seedlings showed tolerance to salinity levels between

12 and 19 dS m^{-1} (Tomar and Gupta, 1985), seedlings grew well at 16.3 dS m^{-1}, but could not tolerate salinity stress of 32.5 dS m^{-1} (Singh, 1990), grew at 18.5 dS m^{-1}, with the caveat that 25-year-old trees were only 5m tall with a collar diameter of 44 cm (Singh and Jha, 1993), and had a 63% survival rate at 10 to 12 dS m^{-1} (Patil et al., 1996).

More recently, studies focused on understanding Pongamia salinity tolerance mechanisms at physiological and molecular levels. Salinity tolerance ranges varied from ~5 to 50 dS m^{-1} (Arpiwi et al., 2013a; Marriboina et al., 2017, 2021; Marriboina and Attipalli, 2020). Findings indicated little or no differences in tolerances among plants from different provenances (Arpiwi et al., 2013a), that key salt-responsive genes and pathways effectively operate in the roots to confer its high salinity tolerance to Pongamia (Marriboina et al., 2017, 2021), and that Pongamia roots act as a barrier/filter of excess Na^+ avoiding accumulation in the leaves (Marriboina and Attipalli, 2020).

Pongamia is also regarded as a drought tolerant species due to its dense network of lateral roots which can extend up to 9 m, and deep tap roots which can extend to up to 10 m (Immanuel et al., 2019; Orwa et al., 2009). There is anecdotal evidence that mature trees between 6 and 10 years old, survived a long period of drought in Australia between 2007 and 2008 (Murphy et al., 2012) but preliminary studies on the effect of drought on seedlings were inconclusive (Biswas et al., 2013). Maximum growth rates have normally been observed in well drained soils with sufficient levels of moisture, with average minimum annual rainfall between 500 and 800 mm, and irrigation during the establishment stage required for optimum development in tropical and subtropical areas (Murphy et al., 2012), with some suggestions that the combined amount should exceed 950 mm per annum in combination with a soil-water holding capacity of 150 mm (Garg et al., 2014; Wylie et al., 2021). However, the physiological attributes conferring drought tolerance to Pongamia are still poorly understood, with only one study exploring its mechanisms and suggesting that adaptive mechanisms make it possible for the plant to maintain normal photosynthetic rates under drought (Immanuel et al., 2019).

The utilization of marginal land for large-scale Pongamia plantation is at the centre of its success as it would eliminate competition with fertile land for biofuel production. Plants have several different morphological, physiological, and biochemical responses under salt and drought stress, and these are not yet fully understood in Pongamia. Several engineering tools are available so that these mechanisms can be better understood (M. Singh et al., 2021), and these will need to be applied in Pongamia research so results can be used to inform breeding programmes. Also, many questions remain in terms of the levels of salinity and drought Pongamia can withstand and the long-term impact of moderate and high levels of drought and salinity on tree performance, as well as the impact of interactions between different abiotic stresses. Only long-term trials coupled with co-ordinated screening and breeding for salinity and drought tolerance in Pongamia will ensure that large-scale plantations are economically viable.

2.2. Nodulation and symbiotic nitrogen fixation

The nitrogen fixing ability of Pongamia gives it an important advantage over non-legume crops. It relies on the formation of specialised root organs, commonly referred to as nodules, as a result of symbiotic relationships with nitrogen-fixing bacteria collective referred to as rhizobia (Biswas and Gresshoff, 2014). Understanding the mechanisms and regulation of nitrogen fixation as well as the species of rhizobia which can form successful relationships with Pongamia are key for the successful domestication of the species.

Pongamia is reported to form associations with several species from the genera *Bradyrhizobium* and *Rhizobium* and to exhibit a classical legume nodulation response (Arpiwi et al., 2013b; Rasul et al., 2012) (Fig. 3). Nodulation takes place mainly in the upper part of the root systems and it is suggested that since early nodulation supresses the formation of new nodules, sapling inoculation with effective rhizobia strains will reduce the issue of competition from endogenous rhizobia (Murphy et al., 2012).

Fig. 3. Pongamia roots showing nodules as a result of symbiotic associations with rhizobia.

A wide range of rhizobia strains have been tested for their association potential with Pongamia with some contrasting results. For example, *Rhizobium* sp. strain NGR234, which is reported to form associations with more legume species than any other microsymbiont (Schmeisser et al., 2009), has reportedly failed (Pueppke and Broughton, 1999; Samuel et al., 2013) and been successful (Scott et al., 2008) at nodulating Pongamia roots. Other strains have been successful at nodulating Pongamia roots (Table 2). Although these strains could potentially be selected as inocula to reduce N fertiliser inputs in Pongamia production systems, studies quantifying the effectiveness of the strains in promoting atmospheric N fixation are lacking and more in-depth quantification is required in future studies. Additionally, while *Rhizobium pongamiae* VKLR01^T, a novel strain identified in India, has been suggested as a strong candidate for use as inoculum in degraded/marginal land given it is ability to tolerate salt, drought, and alkaline stress (Kesari et al., 2013), and others have demonstrated some degree of tolerance to abiotic stresses (Rasul et al., 2012), studies quantifying the tolerance of rhizobia strains able to form associations with Pongamia to abiotic stresses, as well as heavy metals, are also lacking.

Besides being able to grow in marginal land, Pongamia has the advantage of being able to fix its own N which has multiple implications in terms of climate change mitigation and pollution of both land and water. However, for the full potential of this advantage to be realised, and for this to be translated into reductions or no N application in large scale plantations, there is an urgent need for studies exploring how the nitrogen fixation potential relates to Pongamia nitrogen requirements at a large/long-term scale. Additionally, studies looking at the effect of different rhizobia strains inoculum must consider the ability of different rhizobia strains to tolerate abiotic stresses. This would allow for protocols to be developed in a way that would maximise the potential of Pongamia to grow in marginal, dry areas without relying on fertiliser application, which as mentioned, has large implications for climate change mitigation and pollution as well as for reduction of competition with fertile land for the production of biofuel. See Table 2 for the origin, efficiency, and resistance to abiotic stresses for all strains tested in the studies cited.

Table 2
Rhizobia strains ability to form associations with Pongamia, origin, N fixation ability and resistance to abiotic stresses.

Strain	Form associations ✓ = yes X = no	Sources	Origin	N fixation efficiency/ ability	Resistance to abiotic stress
Rhizobium sp. strain NGR234	X ✓ X	Pueppke and Broughton (1999) Scott et al. (2008) Samuel et al. (2013)	Papua New Guinea	NR	NR
Rhizobium fredii USDA257	X	Pueppke and Broughton (1999)	China	NR	NR
Bradyrhizobium japonicum CB1809	✓ ✓	Scott et al. (2008) Samuel et al. (2013)	USA	NR Inconclusive	NR
Bradyrhizobium sp. CB564	✓ X	Scott et al. (2008) Samuel et al. (2013)	Australia	NR	NR
B. japonicum strain USDA110	✓	Samuel et al. (2013)	USA	NR	NR
ICRISAT-derived strain IC4061	✓	Samuel et al. (2013)	India	NR	NR
ICRISAT-derived strain IC7001	✓	Samuel et al. (2013)	India	NR	NR
ICRISAT-derived strain IC7017	✓	Samuel et al. (2013)	India	NR	NR
Bradyrhizobium yuanmingense[a]	✓	Arpiwi et al. (2013)	Australia	26.5–78.7 %[b]	Temperature (29–39 °C), Salinity (<1% NaCl)
Bradyrhizobium sp. DOA10[a]	✓	Arpiwi et al. (2013)	Australia	26.5–78.7 %[b]	Temperature (29–39 °C) Salinity (<1% NaCl)
Bradyrhizobium sp. ORS305[a]	✓	Arpiwi et al. (2013)	Australia	26.5–78.7 %[b]	Temperature (29–39 °C) Salinity (<1% NaCl)
Bradyrhizobium liaoningense LGM 18230^{T}*	✓	Arpiwi et al. (2013)	Australia	26.5–78.7 %[b]	Temperature (29–39 °C) Salinity (<1% NaCl)
Rhizobium sp. 8211[a]	✓	Arpiwi et al. (2013)	Australia	71.9–85.9 %[b]	Temperature (29–39 °C) Salinity (<1% NaCl)
Rhizobium miluonense CCBAU 41251^{T}	✓	Arpiwi et al. (2013)	Australia	71.9–85.9 %[b]	Temperature (29–39 °C) Salinity (<1% NaCl)
Rhizobium miluonense CC-B-L1	✓	Arpiwi et al. (2013)	Australia	71.9–85.9 %[b]	Temperature (29–39 °C) Salinity (<1% NaCl)
Rhizobium sp. CCBAU 51330[a]	✓	Arpiwi et al. (2013)	Australia	71.9–85.9 %[b]	Temperature (29–39 °C) Salinity (<1% NaCl)
Rhizobium sp. *43015*[a]	✓	Arpiwi et al. (2013)	Australia	71.9–85.9 %[b]	Temperature (29–39 °C) Salinity (<1% NaCl)
Rhizobium pongamiae VKLR01^{T}	✓	Kesari et al. (2013)	India	Yes[c]	Temperature (40 °C) Salinity (up to 4% NaCl)
Bradyrhizobium sp. GX5[a]	✓	Rasul et al. (2012)	India	NR	Temperature (40–45 °C) Salinity (0.5–4% NaCl)
Rhizobium sp. TANU 14[a]	✓	Rasul et al. (2012)	India	NR	Temperature (40–45 °C) Salinity (0.5–4% NaCl)
Bradyrhizobium sp. SEMIA 6434[a]	✓	Rasul et al. (2012)	India	NR	Temperature (40–45 °C) Salinity (0.5–4% NaCl)
Bradyrhizobium elkanii SEMIA 5002[a]	✓	Rasul et al. (2012)	India	NR	Temperature (40–45 °C) Salinity (0.5–4% NaCl)

NR not reported.

[a] Isolates tested in the study are related to these strains (>99%).

[b] Measured as the relative ability of nodulated plants to fix nitrogen over plants fed with a nitrogen source.

[c] The novel strain was found to be a nitrogen fixer using the acetylene reduction assay and PCR detection of a *nifH* gene.

2.3. Arbuscular mycorrhizal fungi

Arbuscular mycorrhizal (AM) fungi are soilborne microorganisms known to form symbiotic associations with most land plants (Kariman et al., 2018). In addition to improving growth through increased nutrient uptake, AM can potentially increase tolerance to abiotic stresses, root pathogens, and have the potential to increase tolerance to contaminated soils (Agus et al., 2018; Begum et al., 2019). The potential benefits of AM can only be harnessed on a large scale through careful selection of compatible species beneficial to plant growth or protecting against metal toxicities. However, while Pongamia is known to form symbiotic associations with AM, there is a considerable gap in knowledge relating to the species which can form beneficial relationships so that they can be used as inoculum as part of management strategies.

Ponpandian and Rose (2018) found that amongst six species of AM investigated, Pongamia had the highest levels of root colonization (88%) and spore density (340/100 g soil). Pongamia also had the highest species richness levels (19) with nine belonging to the genus *Acaulospora*, four to the genus *Glomus*, two to the genus *Gigaspora*, two to *Scutellospora*, one to the genus *Rhizophagus* and one to *Entrophospora*. Kumar et al. (2019) found similar rates of root colonization in Pongamia as per in Ponpandian and Rose (2018) (86.5%) and a lower spore density (54.95/100 g soil). In contrast, only five species were identified colonizing the roots of Pongamia, all belonging to the genus *Glomus*. Another study aiming to identify common AM species from Pongamia's rhizosphere in India, as well as establishing their colonization potential and ability to increase growth in seedlings, Jha et al. (2014) identified 15 species, with *Glomus* being the predominant genus (seven species), followed by *Acaulospra* (four species), *Paraglomus* (one species), *Rhizophagous* (one species), *Sclerocystis* (one species), and *Simiglomus* (one species). Of the 15 species identified, nine were used to test their efficiency in promoting seedling growth and for all growth parameters measured (shoot length, collar diameter, dry weight, phosphorus (P) content and P uptake), results showed no positive impact of any of the species used. The study also calculated the mycorrhizal dependency index, MD (%) = 100 × [(dry weight of treated plant - dry weight of control)/dry weight of treated plant] and except for one species, all results were in the negative range which the study attributes it to carbon losses to the symbiont. However, reductions in growth rates at early stages have been shown to reverse in later stages (Corrêa et al., 2006).

R. irregularis had the highest levels of root colonization (30.6%) followed by *G. cerebriforme* (20.6%) which also had the highest spore population (160/100 g sand), followed by *A. scrobiculata* (59/100 g sand). The three species were the only ones considered successful in colonizing the roots of Pongamia. It was also observed that seeds did not produce fine roots up to 30 days after sowing and the relatively thick roots formed, were not colonized which can be explained by the ability of large seeds to store enough nutrients in their cotyledons and therefore delay the formation of fine roots which consequently delay AM colonization. With that in mind, the authors removed cotyledons which resulted in reduced growth rates but increased MD dependency and some growth parameters in comparison with control treatments. Similarly, Jha et al. (2017) isolated 11 species from the rhizosphere of four biofuel candidates including Pongamia and tested the effect of inoculum on plant growth, P uptake and seedling quality. The study concluded that none of the parameters tested were affected by the inoculation of any of the species used in the study despite all AM species being successful in colonizing Pongamia 's roots. Except for one, all MD values were in the negative ranges again.

There is potential for AM to be included in management strategies to aid the successful establishment of Pongamia plantations at a large scale. However, there is still a long way to go in terms of developing successful protocols including the type of inoculum, rate, and time of application. Additionally, studies looking at the potential of AM to improve Pongamia outside India are lacking and urgently needed.

3. Phytoremediation and metal tolerances

Phytoremediation can be a cost-effective and more sustainable remediation alternative. It has the potential to remove, degrade or immobilize soil contaminants such as heavy metals, hydrocarbons, chlorinated solvents, and pesticides through different processes (phytostabilization, phytodegradation, phytovolatilization and phytoextraction) (Yadav et al., 2018), and the choice of plant is key to ensure its success. The ability to form symbiotic associations with soil microorganisms such as AM and rhizobia, are also vital as contaminated soils are usually deprived of nutrients (Khan, 2005). Given its relatively fast growth rates, high biomass production, vast root system, ability to grow in marginal land, and ability to form symbiotic relationships with soil organisms (Islam et al., 2021), Pongamia is a good candidate for phytoremediation. Additionally, the potential to grow a biofuel crop in degraded land considerably adds to the suitability of Pongamia as a phytoremediation tool as it would make it more economically viable.

Pongamia has been reported to have potential for the phytoremediation of heavy metals from a fertiliser factory effluent, a tannery, arsenic (As), copper (Cu), and chromium (Cr) in different contexts (Abid et al., 2019; Dharmendra Kumar et al., 2017; Kumar et al., 2009; Manzoor et al., 2015; Shirbhate and Malode, 2004). These studies tested the impact of various concentrations of different contaminants in Pongamia seedlings (up to one-year-old) on different parameters, and Pongamia has been classified both as an excluder (retain and detoxify heavy metals in the root tissue) and as a hyperaccumulator (able take up high levels of heavy metals which is translocated and retained in above ground biomass) (Dipesh Kumar et al., 2017) depending on the contaminant (Table 3). Other studies reported that the addition of different strains and concentrations of AM and rhizobia inoculum can potentially enhance the phytoremediation potential of Pongamia (Agus et al., 2018; Budi et al., 2020; Tulod et al., 2012; Yu et al., 2017, 2019) (Table 4). All the studies cited used young plants and large-scale studies on mature trees are lacking. However, preliminary results from an on-going Pongamia plantation in Zambia (Fig. 4), established in 2016 in copper mining tailings, suggests high survival rates and seed production under high soil copper concentrations (up to 6000 mg kg^{-1}) (Warr, 2018), which emphasizes the potential of Pongamia to remediate contaminated land and the need for more research.

Although progress has been made, research is still needed to

Table 3
Contaminants, metal concentrations and key findings from studies on Pongamia phytoremediation potential.

Study	Contaminants	Concentration	Key findings
Abid et al. (2019)	Effluent concentrations from a tannery in Pakistan	Mg: 262 mg L^{-1} Cr: 98 mg L^{-1} Co: 1.1 mg L^{-1} Cd: 0.12 mg L^{-1} (20 and 40 mL L^{-1})	•No differences between treatments and control (tap water) for shoot length and collar diameter. •Leaf area reduced by 38% at the highest effluent concentration. •Dry shoot biomass reduced by 50% on both treatments •Dry root biomass increased by 90% at the highest concentration level. •Pongamia was categorized as a Cr excluder based on the metal translocation strategy in the plant
Kumar et al. (2009)	Cu, Cr	Cu: 50, 100, 200, 300, and 400 μM Cr: 100, 200, 400, and 600 μM	•*In vitro* experiment •Growth parameters measured on seedlings exposed to all Cr concentrations were not affected •Cu negatively affected root growth •Highest accumulation of Cr was found in the seed coat followed by root, leaves, and cotyledons •Highest amounts of Cu were found to accumulate in the seed coat followed by leaves, roots, and cotyledons.
Kumar et al. (2017)	As	Sodium arsenate (Na_2HAsO_4. $7H_2O$): 0, 0.2, 0.5, 1.0, 1.5, and 2.0 mM	•Pongamia was able to tolerate levels of up to 1.0 mM with no reductions in growth or chlorophyll content •Significant reductions were found at 1.5 mM •Arsenic exposure led to increased antioxidant activity and nutrient accumulation •Pongamia was categorized as an As hyperaccumulator
Manzoor et al. (2015)	Effluent from a fertiliser factory in Pakistan	Mg: 65 mg L^{-1} Cd: 0.11 mg L^{-1}	•Increases in shoot length, number of leaves, leaf area, and number of brunches at low concentrations (10 and 50%) in comparison to controls (irrigated with tap water) • All growth parameters (root and shoot length, fresh and dry root mass, fresh and dry shoot mass, leaf area, number of branches, number of leaves, and collar diameter) decreased with higher levels of effluent concentration.
Shirbhate and	Landfill waste soil	Cu - 0.09 mg g^{-1} Zn - 0.15 mg g^{-1} Cr - 0.05 mg g^{-1}	•Pongamia 2-month-old seedlings grown on landfill waste containing

(*continued on next page*)

Table 3 (*continued*)

Study	Contaminants	Concentration	Key findings
Malode (2004)		Ni - 0.01 mg g^{-1} Fe - 0.21 mg g^{-1} Mn - 0.15 mg g^{-1}	heavy metals significantly reduced the heavy metal concentration in the soils except for Fe •Fresh weight of root and shoot were higher in the plants grown in the waste soil relative to controls because of higher nutrient content in the waste soils •Chlorophyll content in the plants had an inverse relationship with heavy metal absorption •Contaminants were accumulated by the plants vascular and cortical tissues.

understand the levels of tolerance to different contaminants, the mechanisms underpinning these, the role of symbiotic association in facilitating the process and the effect it has on tree survival, growth rates, flowering, and yields. Additionally, to our knowledge, there are no studies looking at the concentration of contaminants in the oil produced by Pongamia grown in contaminated land as well as the fate of these contaminants during combustion which are essential to ensure that Pongamia can be simultaneously used as a phytoremediation tool and as a source of biofuel.

4. Genetics, elite tree selection and propagation

4.1. Genetics and genomics

Pongamia is a diploid species with very limited information on genetics and genomics in public domain. The average nuclear genome size of Pongamia have been estimated by flow cytometry analysis which indicated that the nuclear DNA content of Pongamia is 2.66 pg with predicted 1C value of 1303 Mb. The genome is organised in 22 chromosomes, corresponding to the diploid level ($x = 11$) (Choudhury et al., 2014; Ramesh et al., 2014). The nuclear genome size of Pongamia is approximately 2.5 times of *Medicago truncatula* genome (480 Mb),

Table 4
Contaminants, metal concentrations, AM and Rhizobia inoculum, and key findings from studies on Pongamia phytoremediation potential.

Study	Contaminants	Concentration	Inoculum	Key findings
Agus et al. (2018)	Open pit coal mining soils (forest soil, mined-out soil, overburdened soil and ready-for-revegetation landfill soil) Fe, Al	Forest soil: Fe: 2.88% Al: 0.1me/100g Mined-out soil: Fe: 0.8% Al: 6.61me/100g Overburdened: soil Fe: 3.39% Al: 29.28 me/100g Ready-for-revegetation landfill soil: Fe: 3.91% Al: 4.5 me/100g	AM inoculum (*G. clarum)* contained 66 spores per g and was applied as three levels: (i) no inoculation, (ii) 2 g plant or approximately 132 spores, and (iii) 4 g per plant or approximately 264 spores.	•Best colonization rates (78.9%) resulted from the combination of the forest soils and 2 g per plant of inoculum •This combination also resulted in the highest growth parameters compared to growth in the mined soil media •Survival rate was 100% on all treatments.
Budi et al. (2020)	Soil from silica post-mining areas containing Al	Al: 690 mg kg^{-1}	MycoSilvi variant 1: *Glomus mossea*; MycoSilvi variant 2: *G.mossea, Acaulospora* sp. MycoSilvi variant 3: *G.mosseae, Acaulospora* sp.*and Gigaspora margarita* 5g inoculum per treatment	•MycoSilvi variant 3, resulted in the highest levels of root colonization (20%) •The addition of lime and compost increased it to 80%. •This combination also resulted in the highest P accumulation, leaf greenness index and total plant biomass •Al accumulation in the plant was not measured.
Tulod et al. (2012)	Cu contaminated soils	2.603 mg kg^{-1}	Commercial vesicular arbuscular mycorrhiza at 2.5 g per pot	•Cu contaminated soils amended with AM and zeolite were the most effective overall •Pongamia accumulate 1220 and 26 μg Cu g^{-1} dry matter in the roots and shoots, respectively •In terms of percentage Cu uptake, this represented only 0.078% •Given the limited translocation of Cu from roots to shoots, Pongamia was categorized a Cu excluder able to immobilize Cu in its roots
Yu et al. (2017)	Iron-vanadium-titanium oxide, V-Ti magnetite mining tailings and nickel (Ni) polluted soils	Ni: 50 mg kg^{-1}	Metal tolerant strain of rhizobia (PZHK1/ *B. liaoningense*)	•Inoculation with PZHK1 formed effective nitrogen fixing nodules in Pongamia's roots •PZHK1 increased growth and metal accumulation capacity of Pongamia •Inoculated plants had a higher rate of translocation and metal removal capacity for Fe, Ni and Cu •Nickel content was above the hyperaccumulator threshold •Fe accumulation was higher than the upper limit of Fe in plants •In the V-T magnetite soils, nodulation was also observed in the non-inoculated treatments •Nodule number and N content was higher in the inoculated plants

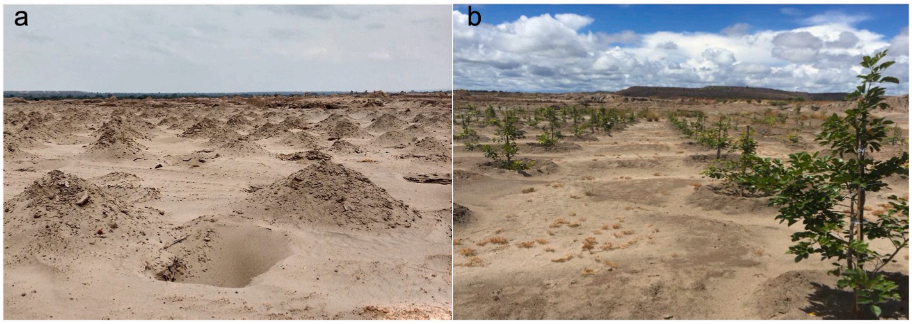

Fig. 4. Pongamia plantation in Zambia, established in 2016 in copper mining tailings under high soil copper concentrations (up to 6000 mg kg^{-1}); **a)** Abandoned tailing storage facility before Pongamia saplings being planted; **b)** Young trees two years after planting.

nearly equal to soybean genome (1107 Mb) and around one-fourth of the size of Pea genome (4802 Mb). Though no annotated nuclear genome sequence of Pongamia has been reported yet (as searched on 18 November 2021), two organelle genomes including Chloroplast (cpDNA) and Mitochondrial genomes (mtDNA) of Pongamia have been sequenced and annotated (Kazakoff et al., 2012). The 152.9 Kb long Pongamia cpDNA contains 77 unique protein-coding genes whereas Pongamia mtDNA that is 425.7 Kb in size and contains 33 unique protein-coding gene. Divergence estimates revealed that chloroplast genes have a higher rate of nucleotide substitution compared to mitochondrial genes. This study also suggests that the nuclear genomes of soybean (*Glycine max*), common bean (*Phaseolus vulgaris*) and mung bean (*Vigna radiata*) are useful resources while attempting to study the Pongamia nuclear genomic environment.

There is paucity of assembled nuclear genome/transcriptome sequencing data for Pongamia in public data repositories, however search in Sequence Reads Archive (SRA; https://www.ncbi.nlm.nih.gov/sra) revealed sequencing datasets submitted in eight studies comprising three, four and one Bioprojects related to whole genome sequencing (WGS) genomic data, RNA-Sequencing (RNA-Seq) transcriptome data and MicroRNA sequencing (miRNA-Seq) transcriptome data, respectively (Table 5). These are unassembled raw reads datasets except the data submitted for BioProject PRJNA274185/PRJNA323432 that reported a Transcriptome Shotgun Assembly (TSA) of Pongamia seed transcriptomes (https://www.ncbi.nlm.nih.gov/nuccore/1036638363). The annotation of TSA revealed 53,586 unigenes, among these 39,602 (73.9%) showed significant similarity to proteins in the NCBI non-redundant databases, and 57.1% of them were classified into 56 Gene Ontology categories. Furthermore, 40.9% of the unigenes were assigned to 128 pathways. The study also identified 364 unigenes involved in five pathways closely related to oil biosynthesis and accumulation. In addition, 5710 expressed sequence tag-simple sequence repeats (EST-SSRs) were also identified out of which 82 EST-SSRs were validated for amplification and polymorphism on 12 Pongamia individuals (Huang et al., 2016). Another transcriptome study on leaf (PRJNA258017) of Pongamia reported transcriptome of 25,146 unique genes, out of 1873 were full length genes. Functional annotation classified genes involved in biological process categories included phosphorylation, metabolic processes, and oxidation-reduction processes. Orthologous gene family analysis conducted using 11 sequenced plant species found 4280 transcriptomes conserved across all species, and 103 unique to Pongamia leaf transcriptome. Pongamia unique gene families included transcripts belongs to ubiquitin-like modifier proteins and BED zinc finger proteins with membership in pathways related to salt tolerance and disease resistance (Wegrzyn et al., 2016). The analysed data for this study is not available in public domain. Another study analysed whole transcriptome of Pongamia (PRJNA299718) to investigate the possible metabolic pathways. The *de novo* assembly (not available in public domain) generated 40,000 contigs and 35,000 transcripts, representing leaf, flower, and seed unigenes. Spatial and temporal expression profiles of photoperiod and floral homeotic genes found GIGANTEA (GI) - CONSTANS (CO) - FLOWERING LOCUS T (FT) as active signal cascade for floral initiation. Pongamia accession (TOIL 1) was used to investigate the temporal expression patterns of key fatty acid biosynthetic genes involved in lipid biosynthesis and accumulation. These findings provide foundation for work on modulation of fatty acid composition and improving oil yields in Pongamia (Sreeharsha et al., 2016).

Table 5

Summary of the Pongamia genomic and transcriptomic datasets found in Sequence Read Archive (SRA) search for data repository of National Centre for Biotechnology Information (NCBI).

Study type/ BioProject	Runs	Size (GB)	Study	Submitter	Year	Reference
Genomic (WGS)						
PRJNA706880	1	0.91	Genome skimming raw sequence reads of 110 IRLC legume taxa	Chinese Academy of Sciences, China	2021	NF
PRJNA552760	3	7.8–13.9	*Pongamia pinnata* cultivar:TOIL1 Genome sequencing	University of Hyderabad, India	2019	NF
PRJNA85127	2	0.21–1.5	*Millettia pinnata* whole genome sequencing	The University of Queensland, Australia	2012	NF
Transcriptomic (RNA-Seq)						
PRJNA433447	9	0.37–0.39	Pongamia seed transcriptome	Shenzhen University, China	2018	Huang et al. (2018)
PRJNA299718	1	0.81	Transcriptome profiling of seed, flower and leaf tissues of *Pongamia pinnata*	University of Hyderabad, India	2015	Sreeharsha et al. (2016)
PRJNA274185/ PRJNA323432	1	4.0	*Pongamia pinnata* Transcriptome or Gene expression	Shenzhen University, China	2015	Huang et al. (2016)
PRJNA258017	1	15.9	*Millettia pinnata* Transcriptome Assembly and Annotation	University of Connecticut, USA	2014	Wegrzyn et al. (2016)
Transcriptomic (miRNAs-Seq)						
PRJNA550227	9	1.4–1.7	Small RNA sequencing of *Pongamia seeds*	Shenzhen University, China	2019	Jin et al. (2019)

NF: Not found.

MicroRNAs (miRNAs) are an abundant new class of non-coding small RNAs and has diverse and important roles in plant growth and development (Bartel, 2004). Recently a miRNA study (PRJNA550227) discovered 236 conserved miRNAs within 49 families and 143 novel miRNAs in Pongamia seeds sampled at three developmental phases. A total of 115 differentially expressed miRNAs (DEmiRs) were identified between successive seed developmental phases. The DEmiR-targeted genes were enriched in the functional categories associated with DNA damage repair and photosynthesis (Jin et al., 2019). The study provides valuable information helpful for future studied on functional characterization in Pongamia. No publications were found citing BioProjects PRJNA706880, PRJNA552760, and PRJNA85127 (Table 5), however raw read datasets provided in the studies can be downloaded and analysed for mining of genomic and transcriptome information through suitable sequence assembly and analysis tools.

The use of markers such as Simple Sequence Repeats (SSRs) (Huang et al., 2016; Shelke et al., 2020), Inter-simple sequence repeats (ISSRs) (Jiang et al., 2017; Sahoo et al., 2010), Amplified Fragment Length Polymorphism (AFLP) (Pavithra et al., 2014; Sharma et al., 2011), Amplified Fragment Length Polymorphism (AFLP) (S. S. Sharma et al., 2016) and Random Amplified Polymorphic DNA (RAPD) in conjunction with ISSR and AFLP (Kesari et al., 2010) have been reported which could be used in marker assisted selection. Winarto et al. (2015) identified four circadian clock genes in Pongamia by mapping its transcriptome short-paired reads library, further improving the understanding molecular mechanisms controlling flowering, and Ramesh et al. (2014) characterised a stearoyl–acyl-carrier-protein desaturase (*MpSAD*) gene responsible for the regulation of seed development. Genes related to salt tolerance have also been characterized in Pongamia. Wang et al. (2013) reported a NaCl-induced gene from Pongamia with the potential to enhance salt tolerance in yeast and Zhang et al. (2021) identified a salt-responsive calmodulin-like gene from Pongamia which has potential application in the production of transgenic salt tolerant crops.

4.2. Cytogenetic factors affecting the genetic stability of Pongamia

Singhal et al. (1990) reported the existence of B chromosomes (Bs) to the tune of 7 numbers in the somatic cells of *Pongamia pinnata*. The mitosis and meiosis of Pongamia is more or less regular with presence of one or two quadrivalents in meiotic Diakinesis to Metaphae-1 as shown by Sarbhoy (1977). Bhatt and Sanjappa (1976) found that the species has five pairs of long chromosomes (3.06–3.90 mm) of which three pairs have centromeres which are approximately median and two pairs have centromeres which are approximately sub-median. The six pairs of short chromosomes (1.70–2.55 mu m) have sub-median centromeres. Eleven bivalents occur at meiosis, and laggards, bridges and cytomixes are common abnormalities probably due to the presence of B chromosomes. Consequently, the percentage pollen fertility was 56.4%. Bs are supernumerary and extra chromosomes/chromosomal fragments present in the cells of Pongamia, causing its genetic imbalance/instability. Bs can be described as "*selfish chromosomes*", a term that has been used for the repetitive DNA which comprises the bulk of the genome in large genome species, except that Bs have a life of their own as independent chromosomes (Jones, 2012). They can accumulate in number by various processes of mitotic or meiotic drive, especially in the gametophyte phase of the life cycle of flowering plants. This parasitic property ensures their survival and spread in natural populations, even against a gradient drive of harmful effects on the host plant phenotype. B-chromosomes are inhabitants of the nucleus, and they are subject to control by "genes" in the A-chromosome (As) complement. This interaction with the As, together with the balance between drive and harmful effects makes a dynamic system in the life of a Bs (Jones, 2012). Appropriate cytogenetic techniques must be developed to selectively eliminate B-chromosomes to ensure positive genetic balance of Pongamia for further recombination breeding.

4.3. Elite tree selection

Pongamia has adapted and grows in a wide range of ecological and edaphic conditions which combined with its outcrossing reproductive strategy, results in a high degree of genotypic and phenotypic variability within the species (Biswas et al., 2013). This high variability poses challenges as traits such as yield, tree architecture, and seed morphology will vary significantly when trees are grown from seeds (Sharma et al., 2011). However, it also provides an opportunity for the selection of elite trees, which are shown by progeny testing to produce superior offspring and therefore display superior traits of interest. Elite trees can then be clonally propagated and cultivated under different production systems (Murphy et al., 2012).

There has been some progress in the development of Pongamia elite trees. Initially, individual trees, referred to as Candidate Plus Trees (CPTs), are selected from a genetically diverse population based on superior morphological and reproductive traits by comparing phenotypic values of a candidate tree with values from a base population or by a scoring method. These selected trees, then serve as a base material for the selection of elite trees through progeny testing and are then used in large scale plantations. Areas of high Pongamia diversity which can be exploited for collection of diverse germplasm have been identified in India (Kaushik et al., 2007, 2015; Kesari and Rangan, 2010; Mukta et al., 2009; Pandravada et al., 2006; Patta et al., 2016; Rao et al., 2011; Sunil et al., 2009, 2012, 2016), Indonesia (Arpiwi et al., 2018; Hasnah et al., 2020), and Australia (Biswas et al., 2013). Full yield potential of Pongamia is achieved once trees are around eight years old (Rao et al., 2011; Sahoo et al., 2011). Pod and seed characteristics have been suggested as a potential secondary selection criteria, however there are contradictory reports on genotypic corelation of seed and pod characteristics with seed oil contents. Kaushik et al. (2007) and Rao et al. (2011) demonstrated a significant positive correlation between seed and pod weight with oil content, suggesting these traits may be effectively used as phenotypic markers, whereas Arpiwi et al. (2013) and Sunil et al. (2016) found that correlation between oil content and seed size is non-significant. Therefore, more research is needed to find the relationships between seed and pod component traits with high heritability before it can be used for the selection of elite trees with the potential for high oil content. Additionally, while the studies cited above and more recent studies (Kaushik et al., 2015; Rao et al., 2019) have identified high-yielding CPTs using morphological markers from different geographical regions, there is paucity of knowledge relating to genotype by environment effect on oil yield and quality traits in Pongamia. Given its broad ecological range, for the full benefits of Pongamia to be harnessed, it is vital that the variation in population genetic structure is investigated across Pongamia geographical ranges.

Selection of elite trees should not be based on pod yield alone since the attribute is highly variable. It is suggested that selection should be based on stable characters that exhibit strong positive correlation/association with kernel yield (Prasad, 2013). Prasad (2013) suggests the following attributes as selection criteria for elite genotypes; (i) appropriate canopy architecture with extended globose canopy, (ii) intensive branching pattern with higher proportion of pod bearing branches, (iii) cluster bearing habit (higher number of clusters of >10 per branch, and more than three pods per cluster), (iv) higher shelling percentage (>40%), (v) resistance to pod-malformation, (vi) higher kernel yield per tree (Prasad, 2013). While Kazakoff et al. (2010) suggests the following; (i) repeated annual cropping, (ii) crop uniformity, (iii) seed mass per tree (yield), (iv) seed oil content (extractable), (v) oil composition and stability, (vi) growth vigour at seedling and adult stages, (vii) erect growth and architecture, (viii) seed abscission, (ix) resistance to insects, nematodes, fungal and bacterial infections, (x) flowering time, (xi) N fixation efficiency, (xii) water use efficiency, and (xiii) hardiness to drought and salinity.

4.4. Propagation

Pongamia can be propagated from seeds. High germination percentages have been reported in different growth mediums including a mixture of sand, soil, and humus (1:1:1) (Arjunan et al., 1994) and sand, soil, and farmyard manure (1:1:2) (Handa and Nandini, 2005). Seed size has been shown to have a positive correlation with higher germination rates and seed quality parameters, given that larger seeds are able to store greater food reserves. However, this only applies to fresh seeds as seed viability starts to deteriorate significantly after three months under storage (Manonmani et al., 1996). For optimal results, seeds should be pre-treated with hot water and planted with the micropyle facing downwards (Rai et al., 1993). Comprehensive information on seed storage, pre-treatment, germination, establishment, transplantation, and abnormalities have been reported elsewhere (Mukta and Sreevalli, 2010).

For propagation from seeds, one important problem which needs attention is the deterioration of seed viability of Pongamia under storage. Seeds from freshly harvested well dried pods show a germination percentage of 70–85%, but seed viability has been observed to decline after four to five months of shelling from freshly harvested pods. Srinivasan (2011) conducted an experiment to elucidate the possible physiological and biochemical changes associated with seed deterioration during Pongamia seed storage. Seed viability pattern, physiological and biochemical parameters were monitored under different storage at regular intervals. Biochemical parameters like electrical conductivity of seed leachates and lipid peroxidation under different treatments showed significantly increased values with seed deterioration. The level of total soluble sugars increased gradually, whereas total soluble proteins and enzyme activity (dehydrogenase and acid phosphatase) decreased with storage period in all the treatments. The optimal conditions for extending seed storability in Pongamia without having any adverse effect on physiological and biochemical parameters were 4 °C and 20 °C, and 33% relative humidity. This study could possibly contribute to more effective storage of Pongamia seeds on a large scale and can be further exploited in other orthodox tree species.

Despite being easily propagated from seed, given the large genetic diversity and long gestation period resulting from seed-derived progeny trees, large scale plantations of Pongamia rely on the development of effective vegetative propagation protocols once superior germplasm is selected. The potential of vegetative propagation in Pongamia has been demonstrated through the use of stem cuttings (Kala et al., 2018; Karoshi and Hegde, 2002; Kesari et al., 2009; Kesari and Rangan, 2010; Palanisamy et al., 1998; Rout and Nayak, 2015a; Sahoo et al., 2021b; Thatoi et al., 2001). These studies identified indole butyric acid as the most efficient growth hormone for inducing roots in stem cuttings of Pongamia. However, optimum success rates seem to be context dependent as they vary considerably depending on whether cuttings are derived from juvenile or mature trees, length of cuttings, propagating medium, genetic response, and season. Although propagation by stem cuttings appears simple and feasible, there are some disadvantages associated with it which include; (i) large mass of stem vegetative tissue is needed, which may not be available for raising large plantations, (ii) the root-system of the stem cuttings can be adventitious or fibrous which does not give adequate anchorage to the plant, (iii) the fibrous root system is always disadvantageous, as it renders plants vulnerable under drought conditions (Prasad, 2021).

Bioenergy Plantations Australia (BPA) has developed a method using young material from mother trees in pots (Wylie et al., 2021). Grafting methods have also showed potential (Kala et al., 2020; Mukta and Sreevalli, 2010; Rout and Nayak, 2015a), and are considered simpler than propagation by cuttings (Mukta and Sreevalli, 2010). The cost of grafting has been reported to be too high to be commercially viable (Mukta and Sreevalli, 2010). However, it is argued that the cost of grafting in relation to the success rate should be considered. For example, cleft-wedge grafting on rootstocks of soft wood results in success rates of 95–100%, thereby reducing the cost per sapling (Prasad, 2013, 2021). Wedge grafting, using young seedlings in polybags as stock and semi-hardwood sections of 12–15 cm length, have shown to be 95% successful with plants producing seeds within three years (Mukta and Sreevalli, 2010). However, seasonal changes can reduce the success rate to 85% (Rout and Nayak, 2015b). More recently, epicotyl grafting has also been used successfully to propagate Pongamia with factors such as age of root stock and season also having an impact on success rates (Kala et al., 2020). However, disadvantages of epicotyl grafting have been reported in other tree species. Despite apparent high initial success following epicotyl grafting in cashew, death of a perceptible number of grafts was observed together with incidence of collar rot disease at subsequent stages (Bhaskara Rao, 1995).

Increased efforts are being put into developing propagation methods through tissue culture which can potentially produce large numbers of clones from a relatively small amount of source tissue through micropropagation/*in vitro* regeneration systems. These regeneration systems are established either through organogenesis or somatic embryogenesis using different explants including buds, meristems, and leaves (Biswas et al., 2013). Mukta and Sreevalli (2010) comprehensively covers the literature on tissue culture studies on Pongamia from the first reports dated from 1997 to 2010. Since then, others have reported successful plant regeneration protocols through different approaches (Belide et al., 2010; Gautam, 2014; Kesari et al., 2012; Shrivastava and Kant, 2010; Tan et al., 2018). However, despite recent developments, BPA reported that after seven years of work on regeneration protocols, they were not consistently reproducible and too costly to be commercially viable (Wylie et al., 2021). Therefore, further improvements in regeneration protocols are still required to ensure that elite trees, once identified, can be used in large scale plantations.

5. Agronomy

5.1. Yield

Pongamia seed yield is highly variable and despite its ability to tolerate a broad range of climatic and soil conditions, and to be cultivated on marginal land, information on the effect of abiotic stresses on yield is lacking and urgently needed. Reports of seed yields in India vary from 9 to 90 kg per tree per year (Rao et al., 2011), in Australia from 20 to 80 kg per tree per year (Abadi et al., 2016; Murphy et al., 2012), and a study from Bangladesh reported that yields vary from 25 kg per tree per year for 15 year old trees to over 100 kg for 20 year old tress, with projections of 300–500 kg of seeds per tree per year, once trees are over 30 years old (Rahman et al., 2014).

A recent study by (Dalemans et al., 2022) using field observations and predictive models, stressed that given the huge variation in Pongamia yields, monitoring long-term yields and mechanisms is vital before Pongamia can be labelled a sustainable and profitable biofuel feedstock. It is also reported that a large proportion of wild trees might not flower at all (Sharma et al., 2011), stressing the need for genetic improvement programmes. Additionally, management practices such as irrigation, fertiliser application, pest control and pollination management can improve Pongamia yield potential, but these are generally context dependent and poorly understood. Therefore, long term field trials from different regions are necessary so that standardised management practices can be developed. Other factors which are likely to impact yield include periods of heavy rain during flowering leading to flower damage and a reduction in pollination, low temperatures during leaf initiation, and extreme weather events such drought, heat, floods, and frost (Abadi et al., 2016; Wylie et al., 2021). Knowledge gaps in Pongamia yields variability and how external factors affect Pongamia yields need to be urgently addressed and are key for the success of Pongamia as a source of sustainable biofuel feedstock.

5.2. Irrigation

Despite its drought tolerance, irrigation may benefit Pongamia yields in dry tropical and subtropical areas. It can improve survival rates of young trees during the establishment phase and may help to increase seed set (Murphy et al., 2012). In Australia, there are reports of trees aged between 6 and 10 years old, surviving for four months without rain during the 2007–2008 drought in a plantation with no irrigation. However, growth parameters (height and diameters) were negatively affected when compared to irrigated trees (Murphy et al., 2012). A report by Wylie et al. (2021) suggests that for optimum yields, soil water storage capacity should be 150 mm with additional rainfall and irrigation in excess of 930 mm per year in plantations in Queensland, with an additional 100 mm for clay and 200 mm for sandy soil. They reported an additional weight of 0.4 g per seed on trees which had their water requirements fulfilled in comparison with trees which went through a drought phase, which translates into an extra yield of 6 kg per tree assuming an average of 15,000 seeds per tree. In India, Pongamia water requirements were estimated to be 950 mm per year in semi-arid regions based on calculations of crop coefficients which takes into account crop transpiration and evaporation (Garg et al., 2014).

The production technology of Pongamia is orientated towards establishing plantations on drylands without irrigation as conventionally no irrigation is needed to grow Pongamia (Prasad, 2021). However, in recent years there is a tendency to produce Pongamia under high input conditions with irrigation, added nutrients and higher tree densities. In Australia, high-density planting of 606 trees per hectare (6 m × 2.75 m) is now being suggested as a way to improve income in years 4–12 of plantations (Wylie et al., 2021). With the availability of Pongamia genotypes for smaller sized trees, there would be a need to identify much closer spacing, so that it could be possible to accommodate a higher plant population density even under dryland conditions that depend exclusively on rainfall. Production technology for elite Pongamia plantation under rain fed dryland conditions of India is reported by Prasad (2021). Harvesting guidelines are described by Dalemans et al. (2022).

5.3. Fertiliser

Pongamia is a legume and therefore can fix atmospheric N. However, not much information is available in terms of N fixation rates and how these affect fertiliser requirements for Pongamia which has big implications in terms of climate change mitigation, and it is argued that the popular perception that Pongamia can grow with little, or no fertiliser does not apply to commercial cultivation as repeated harvest would deplete the soils (Murphy et al., 2012). Nitrogen has been found to be a critical limiting factor during the plant's establishment phase and a rate of 15 g plant^{-1} of N fertiliser for seedlings during the nursery stage has been suggested to improve above ground biomass production, while a lower rate of 5 g plant^{-1} favoured root growth suggesting differences in allocation patterns depending on resource availability. Unlike biomass, nutrient distribution (N,P,K) within the plant and nutrient use efficiency varied depending on the seed provenance highlighting the need for a better understanding of the interactions between genetic variability and environmental factors in Pongamia (Sahoo et al., 2021a). Murphy et al. (2012) also suggest that fertiliser at the seedling stage might enhance establishment and early growth, but based on observations in Australian trials, it may not always be necessary, and the addition of P, K, and micronutrients may be needed in the long term. However, it is suggested that fertiliser regimes should rely on soil and foliar analyses at plantation sites to be effective. Monitoring the nutrients removed from the soils is also suggested as a way to maintain the necessary rates for optimum growth in Pongamia plantations (Wylie et al., 2021). Most of nutrients removed from the soil will still be present in the meal after the oil extraction process and these have been calculated by Osman et al. (2009) based on 12 kg ha^{-1} of seeds/tree x 606 trees/ha x 60% meal = 4.36 t/ha of meal. Based on this, the suggested fertiliser requirements to replace removed nutrients would be 17 kg of P ha^{-1} equivalent to 77 kg of Monoammonium phosphate (MAP) which is a widely used source of P and N with 22% P, and 56 kg ha^{-1} of Muriate of Potash containing 50% K. As for nodulation, high N rates (>80 kg ha^{-1}) have been found to suppress nodulation in Pongamia seedlings and a dose of 40 kg ha^{-1} of N split into two equal doses at the nursery stage was suggested as being optimal both in terms plant growth and nodulation increase (Chaukiyal et al., 2013). Application of N:P:K at the rate of 37:250:125 mg plant^{-1} in ploy pot in nursery was found to be optimum fertiliser dose to obtain maximum root and shoot length and dry weight of seedlings (Jerlin and Vadivelu, 2010).

5.4. Pest, diseases and weed control

Several pests have been recorded to cause damage to Pongamia including pod and stem borers; foliage, sap and bark feeders; locusts; green ants; rabbits; and fungi, mainly in India and Australia (Kumari et al., 2020; Murphy et al., 2012; Orwa et al., 2009; Sundararaj et al., 2005; Wylie et al., 2021). Details of biotic inflictions on Pongamia are described elsewhere (Prasad, 2021). While most of these are not economically important as they do not appear to cause significant damage, others require appropriate management. In Australia, rabbits have been observed to cause seedlings mortality by ring-barking the lower 20 cm of the stem and need to be fenced out from plantations for the first three years (Murphy et al., 2012). Red shoulder leaf beetle (*M. australis*) can cause significant damage to young leaves and flowers and Bulldock® 25 EC, a commercial insecticide, has worked in trials as a control measure, with the caveat that it is highly toxic to bees, so alternatives might need to be found (Wylie et al., 2021). A type of unidentified leaf miner has also been shown to cause significant damage in Australia if found in high numbers, and systemic insecticides have shown to be effective, again with the caveat that these can potentially harm bee populations (Wylie et al., 2021). The fungus *Phyllachora pongamiae*, which causes 'tar spot', has been found to infect Pongamia both in India and Australia and although not a problem in mature trees, can have a more significant impact on seedlings (Murphy et al., 2012). In India, other fungus species are also reported to cause damage mainly at the nursery/seedling stage. Several species are found to cause leaf spot and blight (*Fusicladium pongamiae, Microstroma pongamiae, Phyllochora pongamiae, Robillarda makatii, Urohendersonia pongamiae, Cercospora pongamiae* and *Sphaceloma pongamiae)* and foliar spray of Bavisitin fungicide (0.1%) was found to be effective. Some species cause leaf rust (*Ravenelia hobsoni and Ravebelia stictica)* and can be controlled with sulphur-based fungicides (0.05%). *Oidium* spp. can cause powdery mildew disease which can also be managed by Bavisitin at a lower concentration (0.01%) (TNAU, 2016). Fungal infections can also be a problem in poorly stored seeds (Orwa et al., 2009). Also in India, the gall inducer *Asphondylia pongamiae* has been shown to cause significant damage to seed production in mature trees (Sundararaj et al., 2005) and biological control measures using natural enemies of *A. pongamiae* have been suggested (Devaraj and Sundararaj, 2014). In addition, the use of resistant cultivars have also been explored (Kabber and Javaregowda, 2017). A Phanerogamic parasite *Dendrophthoe falcata* (Loranthaceae) parasitic plant has been observed on Pongamia in India (Prasad, 2021) and in Southern Tamil Nadu (Selvi and Kadamban, 2009).

Weeds can be an issue during establishment stage when seedlings are less than 30 cm tall. Therefore, it is suggested that seedlings should be transplanted to the field only once they are 50–60 cm in height to improve survival (Venkatesh et al., 2003). Poor weed control may lead to delays in the first harvest by one year (Wylie et al., 2021). Both mechanical and chemical weed control measures are said to be critical during the establishment phase (first three years). The use of weed mats are also suggested, however these can be costly (Murphy et al., 2012). Atrazine, a pre-emergence herbicide have been shown to be effective at controlling broad leaved weeds with no negative impact on Pongamia seed germination and seedling growth at a concentration of 0.1–0.2% (Poomaruthai et al., 2013). Increasing tree density is also likely to reduce weed pressure and the need for weed control (Wylie et al., 2021).

5.5. Basal stem sprouts

The sprouts/suckers which arise periodically at the basal part of the stem hinder efficient management of plantations (Csurhes and Hankamer, 2016). If left unchecked, the plant can turn stunted with poor growth of the canopy which is very important for realising yield. Currently, the basal sprouts are being removed manually, to keep the main stem clean and healthy. The manual operation is expensive and time consuming, which may be suited to small plantations of less than 2 ha. Instead, herbicidal treatments can provide a cost effective and efficient control of basal sprouts, especially in large plantations.

Basal bark herbicide is applied using a low-pressure backpack sprayer to thoroughly wet the lower 30–40 cm of the stem using a solid cone or flat fan nozzle. To be effective, it is important to thoroughly wet the entire stem, root collar area, and any exposed roots. Basal bark herbicides use an oil carrier (commercially available basal oil, diesel fuel, no. 1 or no. 2 fuel oil, or kerosene) to penetrate the bark. Trees with thick or rough bark may require increased coverage to be effective. Numerous products are registered for use as basal bark applications. Triclopyr ester is the most used herbicide for the control of suckers in Pongamia. It is found in commercial products such as Garlon 4 Ultra and Relegate. Triclopyr ester is a systemic herbicide, absorbed by the plant and translocated to tissues remote from the point of application. Triclopyr works by disturbing plant growth. It accumulates in plant meristems, cells where growth takes place, causing uneven cell division and growth.

5.6. Pollination management

Pongamia commonly flowers after four to five years after planting and usually flowers one season a year. However, exceptions where two flowering events occur in one year or of precocious flowering have been reported (Murphy et al., 2012). In order for pollination to occur, the keel has to be depressed so that the stigma and anthers can be exposed, commonly referred to as tripping (Raju and Rao, 2006). Pollination management is key for optimum yields. Introduction of beehives has been shown to increase seed production from 37% to 82% (Arpiwi et al., 2014). Flowers only open for one day during anthesis but develop at different stages along inflorescences, which is thought to be an adaptation to adverse weather conditions. However, prolonged periods of heavy rain during flowering can severely impact yields as it will limit pollination rates (Wylie et al., 2021). Pongamia is primarily dependent on bees for pollination with *Apis* sp., *Amegilla* sp, *Megachile* sp., *Xylocopa* sp., and *Nomia* sp. being recorded as effective pollinators (Arpiwi et al., 2014; Raju and Rao, 2006; Shankar et al., 2017; Veereshkumar et al., 2020). Other species of bees, wasps and thrips have also been recorded visiting Pongamia flowers but they are either occasional visitors or classified as nectar or pollen thieves, and therefore are not considered to be effective pollinators of Pongamia (Raju and Rao, 2006; Veereshkumar et al., 2020). To our knowledge, no comprehensive information is available on the optimum hive density to ensure pollination services in large scale plantations. One hive per hectare has been suggested as being adequate (Wylie et al., 2021), but more research is needed to establish optimum pollination rates in different contexts, especially in terms of how pollination affects yields in different varieties given Pongamia's large genetic variability.

6. Biofuel potential

6.1. Biodiesel

Many studies have examined the suitability of Pongamia oil as a source of biofuel (Bala et al., 2011; Bobade and Khyade, 2012; Cox et al., 2014; Fu et al., 2021; Karmee and Chadha, 2005; Khayoon et al., 2012; Meher et al., 2006; Raheman and Phadatare, 2004; Sahu et al., 2011; Scott et al., 2008; Sharma and Singh, 2008). Oil content varies between 15 and 45% depending on the provenance and in terms of oil content, elite trees are selected on the basis of ~40% (Arpiwi et al., 2017; Fu et al., 2021; Kesari et al., 2008; Kumar and Kaushik, 2015; Mukta et al., 2009; Patel and Sankhavara, 2017; Wylie et al., 2021). The presence of toxic flavonoids means Pongamia oil is not fit for human consumption (Meher et al., 2006) so Pongamia has been classified as a second-generation biofuel which are produced from non-food crops thereby reducing competition with arable land. However, it is unknown how Terviva® (https://www.terviva.com) patents to refine crude Pongamia oil into food-grade vegetable oil (see section 8) is likely to affect this, and depending on the level of investment in Pongamia in the coming years, land and water competition might become an issue.

The last decade has seen an increase in research into the commercial viability of Pongamia as a biofuel feedstock with economic assessments yielding mixed results. Abadi et al. (2016) concluded that Pongamia was unlikely to become commercially viable as a biofuel feedstock in Australia, mainly due to uncertainties around yield. Dalemans et al. (2019) argued that Pongamia cultivation in India had limited financial potential with biodiesel as the end-product, suggesting that it could only be profitable at a small scale unless there were efforts to optimise mechanization, yields and agroforestry set-ups. Prasad and Singh (2020) found that biodiesel production from Pongamia is an economic viable option in the Pacific Island of Vanua Levu both at a small and large scale. Klein-Marcuschamer et al. (2013) concluded that biorefineries processing Pongamia seeds for aviation fuel in Australia would be competitive with crude oil, and Halder et al. (2014) concluded that biodiesel production from Pongamia could reduce fossil fuel based diesel imports by 21.67% in Bangladesh.

Despite uncertainties surrounding the economic viability of Pongamia as a biofuel feedstock, several companies have recently invested in Pongamia as a source of biofuel including Investancia, BPA Australia, Tree Oils Limited, Cleanstar Energy, Betterworld Energy, and PHYLA Earth. Also, a recent report presenting a preliminary economic study by Wylie et al. (2021) reports interest in Pongamia from Japanese power generating companies, Qatar Airways, and cattle companies. The report offers a foundation for a Pongamia industry viability assessment and argues that while more research is needed, there is enough practical knowledge and information to be used as a basis for further investigations into the commercial viability of Pongamia.

A recent comparative study by Mitra et al. (2021) which reviewed the environmental and socio-economic aspects of three biofuel candidates including Pongamia, argues that biodiesel production will only be economically viable when the by-products can be converted into value-added products and argues for a circular bioeconomy approach. A circular bioeconomy requires that economic development is balanced with environmental protection and given the multiple applications of Pongamia, if research and breeding efforts are done in a collaborative manner and are targeted at filling the necessary gaps, including further research on by-products (see sections 6.2 and 10), it could play an important role in the promotion of sustainable development goals (Gigliotti et al., 2019).

6.2. Biogas

Biodiesel production from Pongamia generates 7.88 kg of biomass waste per kg of biodiesel, mainly in the form of pods and seed cake. Total energy (expressed in megajoules) of the biomass waste has been estimated to be 3.46 times higher than the energy of 1 kg of biodiesel (Khuntia et al., 2017). This provides a great opportunity for an integrated valorisation pathway as the biomass waste can potentially be used as anaerobic digestor's feedstock for biogas production. The digestate produced, can in turn be used as organic fertiliser given its high N content (Mitra et al., 2021). A Indian study, concluded that Pongamia residues produces more biogas than other commonly used oilseed trees such as *Jatropha curcas,* and that the sale of biogas can lead to economic returns 2 to 3 times higher than the direct sales of residues, potentially reducing biodiesel production costs by 30–80% (Khuntia et al., 2017). This could give Pongamia derived biodiesel a competitive advantage over diesel in financial terms as well as reduce emissions. However, biogas yields from Pongamia residues vary (Chandra et al., 2012; Khuntia et al., 2017; Mitra et al., 2021). Gunaseelan (2014) developed a model which could estimate biodegradability based on biochemical characteristics. The model predicted the biodegradability of previously published biomass waste ($r^2 = 0.88$) from their biochemical composition which could be used to predict biogas yields from Pongamia residues. Ultimately, the utilization of Pongamia waste in biogas digesters not only can influence the economics of biodiesel production but it can also contribute to a circular bioeconomy benefiting the environment.

6.3. *Pongamia seed oil characteristics*

Pongamia oil is extracted from the seeds by expeller pressing, cold pressing, or solvent extraction (Berk, 2013). The oil is yellowish-orange to brown in colour and can be used to produce biodiesel through the process of trans-esterification. The yield of methyl esters from the oil under the optimal conditions is ~97–98% (Yadav et al., 2018). Fatty acid profile (Usharani et al., 2019) and physical and chemical properties of Pongamia oil (Karikalan and Chandrasekaran, 2015) are provided in Table 6:

7. Agroforestry potential

Pongamia stands out in agroforestry programmes as compared to several other tree components due to its soil enhancing properties (Prasad, 2021; Wani et al., 2009; Wani and Sreedevi, 2007). It has been integrated in silvopastoral systems, which combines forestry, forage crops, and livestock, especially in semi-dry regions in India (Singh and Roy, 1993) where it is also commonly used in farm boundary plantations (N. Sharma et al., 2016). These clusters of trees might have been planted intentionally but more often than not, they are retained by farmers either scattered across crop fields or along the border (N. Sharma et al., 2016).

The inclusion of Pongamia in agroforestry systems has been suggested as an effective way to sequester carbon dioxide from the atmosphere and for the bio-amelioration of salt-affected land while providing socio-economic benefits to small scale farmers (Atangana et al., 2014; Handa et al., 2020; Nair, 2007; Pragya et al., 2017; Singh, 2017; Swamy et al., 2017). It has also been suggested that bee-keeping can add considerable value to these systems as Pongamia is a good source of pollen and nectar to honey bees (Daisy et al., 2001; Shankar et al., 2017; Usharani et al., 2019).

Table 6
Fatty acid profile, and physical and chemical properties of Pongamia oil. Adapted from Usharani et al. (2019) and Karikalan and Chandrasekaran (2015)

Fatty acid profile		Physical and chemical properties		
Fatty Acid	Content (%)	Properties	Unit	Test Value
Palmitic acid	3.7–7.9	Density	kg/m^3	0.927
Stearic acid	2.4–8.9	Kinematic viscosity at 40 °C	mm^2/s	40.2
Oleic acid	44.5–71.3	Acid value	mg KOH/g	5.40
Linoleic acid:	10.8–18.3	Pour point	°C	6
Linolenic acid	2.6	Cloud point	°C	3.5
Arachidic acid	2.2–4.7	Flash point	°C	225
Eicisenoic acid	9.5–12.4	Calorific Value	MJ/kg	8742
Behenic acid	4.2–5.3	Carbon residue	Wt.%	1.51
Lignoceric acid	1.1–3.5	Specific gravity		0.936

Pongamia intercropping with drought resistant annual crops such as castor (*Ricinus communis*), pigeon pea (*Cajanus cajan*), cowpeas (*Vigna unguiculata*), green gram (*Vigna radiata*), sesame (*Sesamum indicum*), cluster beans (*Cyamopsis tetragonoloba*), horse gram (*Macrotyloma uniflorum*), niger (*Guizotia abyssinica*), sunflower (*Helianthus*), and fodder grasses, has been recommended depending upon the local conditions in inter-row spaces of the plantation in the first three years. Intercropping of grain crops may not be possible after three years of establishment of Pongamia plantations due to its canopy expansion (Prasad, 2021), although it is argued that an effective canopy management regime (i.e. pruning), could mitigate this (Daniel and Hegde, 2007). Foliage yielding crops like forage grasses and essential oil yielding grasses like lemon grass (*Cymbopogon citratus*) and Citronella (*Cymbopogon nardus*), could be grown even after Pongamia trees develop extended canopy (Prasad, 2021).

Pongamia intercropping with pigeon pea was shown to improve soil physicochemical properties resulting in higher intercrop yields (Banerjee et al., 2013). Studies conducted by the ICAR - Central Agroforestry Research Institute have shown that castor (*Ricinus communis*) can be successfully intercropped with Pongamia planted at 5m × 5m spacing resulting in higher yields of castor beans (Dhyani et al., 2015). Other crops such as cowpea, groundnut and black gram could be successfully intercropped with Pongamia spaced at 6m × 6m, while intercrops like sorghum, pearl millet, pigeon pea, soybean, mung bean, chickpea, sunflower, and safflower could be successfully intercropped with Pongamia without reductions in yields in comparison with monocultures, during the initial four years. Pongamia intercropping systems also have resulted in improvements in soil organic carbon and available N, P, K as compared to sole cropping. However, with lower net returns mainly because during initial years, establishment of Pongamia plantations result in expenditure, without any economic return (Kaushik et al., 2016; Wani et al., 2009). However, although it is argued that the cost of establishment can potentially be met through intercropping during the gestation period of Pongamia plantations (Kaushik et al., 2016), a study evaluating the profitability of Pongamia agroforestry systems using a case study from India, suggested that it has limited financial potential and is only profitable to a sub-set of small-scale farmers in the middle to long term (Dalemans et al., 2019).

Two companies globally are proposing to integrate Pongamia into sivopastoral systems, Investancia (https://investancia.com/), and PHYLA Earth (https://www.phyla.earth/). PHYLA Earth has its operations focused in Sub-Saharan Africa and India, and is proposing reafforestation agroforestry and silvopasture Pongamia systems. Investancia is a company based in the Netherlands with a business model aiming to reforest 2500 ha of degraded land in the Gran Chaco region in Paraguay, with the oil produced from these silvopastoral systems classified as having low or even negative indirect land use change (ILUC) value due to its N-fixing capacity (Wylie et al., 2021). However, a study investigating the nutrient status of Pongamia intercropped with soybean and safflower (*C. tinctorius*) in India, found that nutrient concentration in Pongamia varied significantly among different seed sources (Inamati and Shahapurmath, 2019) and another Indian study in a silvopastoral system, found that different fertiliser and pruning regimes varied significantly in terms of impact on yield (Divakara et al., 2021).

Research to date has shown considerable potential of Pongamia as an agroforestry component. However, there is a clear need for increased coordination among stakeholders for a more targeted approach aiming to develop standardised models for the successful cultivation of Pongamia in different contexts. More information is needed to inform farmers about the right combination of crops, tree density/spacing and management practices which can make the system financially viable. Additionally, promoting Pongamia's integration in agricultural landscapes will require an in-depth understanding of local stakeholders' perceptions as social factors are shown to have a stronger impact than biological ones on the decision to integrate agroforestry systems both in intensive and extensive agricultural landscapes (Laroche et al., 2018).

8. *Food security and socio-economic benefits*

While most of the attention on Pongamia in recent years has focused on its potential as a sustainable source of biofuel, and the vast majority of literature refers to Pongamia as a non-edible crop, recently, Terviva® has invested in research and development to cultivate and market Pongamia as a sustainable food source. After ten years of trials in North America, initially using elite trees from Australia, the company has patented technologies to process Pongamia seeds into edible grade protein for both human and animal consumption, and to refine crude Pongamia oil into food-grade vegetable oil (Terviva, 2020). In comparison with other oil and protein crops, except for palm oil, Pongamia yields are higher than most (Ritchie and Roser, 2021), which combined with its ability to grow in marginal land, has huge implications for food-security at a time where sustainable food sources are vital. However, this might reduce Pongamia value as a biofuel feedstock given the debate surrounding the use of land for food vs fuel. It remains to be seen what part Pongamia will play as a sustainable food source and whether in the case of Pongamia, food security and sustainable biofuel production can be complementary.

Although Pongamia seed cake, the by-product of the oil extraction process, is rich in protein, is not normally used as a source of animal feed due to the presence of anti-nutritional factors (ANFs) such as phytates, saponins, karanjin and pongamol (Gopan et al., 2020). However, the Central Food Technology Research Institute (CFTRI) in India argues that the simple process of acid hydrolysis, can remove ANFs which would make Pongamia cake comparable to soybean meal in terms of quality (Soren et al., 2009; Vinay and Kanya, 2008). It has already replaced 50% of soybean meal in lambs without affecting their metabolism (Rao et al., 2016) and has a great potential to become a sustainable source of animal protein. The plant nutrient composition of Pongamia cake is as follows: Nitrogen (4.8%), Phosphorous (0.4%), Potassium (0.74%), Calcium (0.25%), Magnesium (0.17%), Zinc (0.0059%), Iron (0.1%), Copper (0.0022%), Manganese (0.0074%), and Boron (0.0019%) (Osman et al., 2009).

Pongamia can potentially also bring socio-economic benefits to stakeholders as the opportunity to restore degraded and contaminated land provides opportunities for local communities around these areas. PHYLA Earth which works with regeneration of degraded land, has successfully implemented a pilot project covering 4 ha of a copper mining tailing site in the Copperbelt region of Zambia, with a 99% survival rate of Pongamia elite trees planted in 2016. Through a business model which engages actors from government and large-scale farmers to NGOs and small farmer cooperatives, they have started generating jobs to local communities in areas where the degraded land left as a legacy of the mining industry is unsuitable for most forms of agriculture. In addition to the potential environmental benefits already mentioned, their approach aims to create new post-mining circular bioeconomies, with jobs that last beyond the revegetation process, through the production of bioenergy, bio-pesticides, bio-pharmaceuticals, organic fertilisers and, animal feeds with potential to benefit marginalised communities and have a gender positive impact given that approximately 40% of smallholder farmers in Zambia are women (FAO, 2018).

9. *Climate change mitigation potential*

Plants yielding biofuel such as Pongamia can potentially mitigate climate change through CO_2 sequestration. The CO_2 sequestration potential of Pongamia during the 10–15 years of its growth has been found to be many folds that of several other tree species (Prasad, 2021). Pongamia was found to sequester around 45–50 kg of C per tree per annum as against 28–35 kg of Neem (*Azadirachta indica*), 23–26 kg of Mahua (*Madhuca latifolia*) and 11–15 kg in respect of Tendu (*Diospyros melanoxylon*) (Chaturvedi et al., 2011; Gera and Chauhan, 2010; Gupta, 2009; Karmakar et al., 2012; Moore, 2009; Reddy et al., 2009).

It has been suggested that a population of 200 trees (aged 20 years) in an area of 1 ha can sequester ~15 tonnes of carbon (Vayugrid, 2014). Estimates by the Council of Scientific & Industrial Research (CSIR) in India, indicate that this could equate to 25 t h^{-1}. A study carried out in 2006 estimated that over the course of a 25-year period, one Pongamia tree has the potential to sequester 767 kg of carbon. The carbon sequestration ability of Pongamia was calculated for 3600 trees planted in the Powerguda village in Adilabad district of Telangana State in India. The certified carbon emission reduction was sold to '500 ppm GmbH', a German environmental group (Pongamia for Bioenergy and Better Environment). The reduction came from replacing diesel fuel with natural oil from Pongamia seeds (Dsilva, 2003). The purchase was effected for ten years' supply of emission reduction from 140,000 kg of Pongamia oil, worth $4164. According to a USA based Company Terviva®, over a span of thirty years of its life, a single acre of Pongamia can sequester up 115 tons of carbon and one acre of Pongamia can replace one acre of oil palm plantation or up to four acres of soybean. Terviva® argues that the food products developed using Pongamia would be carbon negative since the trees sequester more carbon than the beans that produce in emissions from field to plate (Neo, 2020).

10. Other applications and uses

Pongamia has a large number of applications, and among those, its medicinal value has been recognised for decades with its roots in Ayurvedic medicine and comprehensive information on Pongamia medicinal uses, phytochemistry, and pharmacology can be found elsewhere (Al Muqarrabun et al., 2013; Bholane and Hiremath, 2020). Beyond its medicinal value, and others valorisation pathways already covered in the review, Pongamia oil and cake can be used as organic fertiliser, has pesticidal activities, can be used as animal feed, and as feedstock for the production of enzymes and metabolites (Sharma et al., 2020). Traditionally, besides the cooking and lighting uses in rural areas, it was used as a lubricant, water-paint binder, in soap making and tanning industries. The oil is known to have value in folk medicine for the treatment of rheumatism as well as human and animal skin diseases. Seed oil is also used in scabies, leprosy, piles, ulcers, chronic fever, lever pain and lumbago (Yadav et al., 2018).

Pongamia produces natural chemical compounds, such as karanjin and pongamol (Fig. 5), which impart bitter taste to the foliage and other parts of the tree. These compounds deter consumption of leaves by herbivores and insect infestations, resulting in lower management costs and enhanced sustainability. In addition, these compounds are valued for use in crop sprays, cosmetics, and sunscreen products. Pongamol and karanjin isolated from the pods of Pongamia possess significant anti-hyperglycemic activity in streptozotocin-induced diabetic rats and type 2 diabetic db/db mice and protein tyrosine phosphatase-1B may be the possible target for their activity (Tamrakar et al., 2008). Karanjin is an

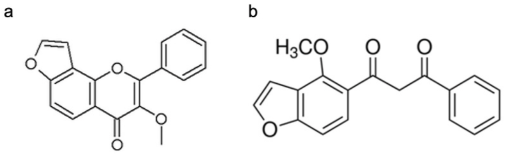

Fig. 5. a) Karanjin, a white crystalline powder, is furano-flavanol (3-methoxy furano-2,3,7,8-flavone) in quantities of 2% by seed weight and 4–5% by weight of oil. **b)** Pongamol is 1-(4-Methoxy-5-benzofuranyl)-3phenyl-1,3-propanedione. It is a pale yellow to cream-coloured powder. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

acaricide and insecticide and is reported to have nitrification inhibitory properties (Majumdar et al., 2004). The resistance of Pongamia trees to termites and to a wide range of other pests is due to karajin and pongamol. Karanjin could potentially be used as an efficient pesticide in organic agricultural programmes where chemical pest control is not allowed (Lale and Kulkarni, 2010). Pongamia oil on an average contains 2–4% karanjin and 0.3–0.9% pongamol. Derisom is a commercial formulation containing Karanjin as a 2% emulsifiable concentrate. Karanjin works as a growth regulator and anti-feedant on the adult as well as nymph pests. Karanjin is a potent nitrification inhibitor which is as effective as other commercial synthetic nitrification inhibitors (Majumdar, 2007). The presence of furan ring (C_4H_4O) is essential for the nitrification inhibitory activity (Saharawat and Mukharjee, 1977). The therapeutic action of Pongamia oil in the management of conditions such as piles, ulcers, and skin diseases is mainly attributed to Karanjin (A. Singh et al., 2021). Shejawal et al. (2014) reported pharmacokinetic parameters of karanjin in rats after oral administration of ethanolic extract of Pongamia. Pongamia oil is also used in cosmetics for its sunscreen activity which is mainly attributed to pongamol (Bernoud et al., 2019). The extraction of karanjin from seeds of Pongamia has been reported by Vismaya et al. (2010). Extraction of karanjin and pongamol from Pongamia oil by reverse phase HPLC has been reported by Gore and Satyamoorthy (2000).

The literature covering the multiple applications of Pongamia is vast and it is beyond the scope of this study to review it in detail. However, for Pongamia to succeed as a sustainable biofuel alternative, it is vital that its applications are considered in a holistic manner. For example, the meal produced after the oil is extracted can be used as animal feed and reduce methane (CH_4) emissions from livestock as well as restore N depleted pastures, and compounds extracted from crude oil can be developed into bio-insecticides (Pant et al., 2016; Wylie et al., 2021). It can also be used as an effective organic fertilizer as it is rich in NPK (4:0.5:0.5) and karanjin (>800 ppm), while at the same time providing protection from insect pests and soil borne pathogens due to its pesticidal activity. Currently, the cake is being widely used on crops like rice, wheat, cotton, sugarcane, vegetables, coconut, tea and coffee plantations, fruit orchards, aromatic oil yielding plants, and golf grounds (Green my life, 2021). Additionally, increases in cotton yield have been linked to the application of Pongamia seed cake when compared to the application of inorganic fertilizers which has great implications in terms of climate change mitigation (Osman et al., 2009).

These multiple applications have potential to form part of a circular bioeconomy with a zero-waste approach, in line with sustainable development goals (Gigliotti et al., 2019). However, it will require multifaceted approaches and collaboration among stakeholders, from small-and large-scale farmers to academics and the industry. Table 1 (Supplementary Material) provides a list of patents on Pongamia different valorisation pathways.

11. Conclusions and recommendations

Research on the multiple applications of Pongamia has grown considerably in the past decade or so and the growing interest in its commercial viability and environmental benefits indicate the potential of this multifaceted, resilient tree to provide benefits to society at a small and large scale. However, many gaps in knowledge still exist and it is vital that future research look into filling these gaps using a more holistic and collaborative approach. Harnessing the multiple applications of Pongamia in a holistic manner with collaboration among key stakeholders is in our view, key for the successful application of its benefits, which as shown here, go way beyond biofuel production.

Our study can act as a source of valuable information for researchers and other actors interested in harnessing the multiple applications of Pongamia and we conclude that Pongamia has potential to form part of a circular bioeconomy, and this should be further explored. Given its multiple applications, Pongamia can form part of a framework that places biomass utilization in a broader context and prioritizes its use for basic human needs and environmental gain. However, this can only be achieved through optimal valorisation of production and consumption of Pongamia biomass using a circular bioeconomy model in line with sustainable development goals. We recommend that future research should therefore focus on how to integrate its multiple applications using a sustainable value-chain approach or similar (Collier et al., 2017). Model-based frameworks for the design of biofuel value chains exist (Villeda et al., 2012) and could be a useful tool in Pongamia research and development. See Fig. 6 for a suggested Pongamia Research Framework based on the findings and recommendations highlighted here.

Research is at the core of the development of sustainable value chains and in the case of Pongamia, co-ordinated breeding efforts are at the heart of this success and future research needs to focus on informing these. Further studies should focus on the variation in population genetic structure across Pongamia geographical range as well as on interactions between genotype, environmental stresses, and yield. Further understanding of the mechanisms underlying its resilience to abiotic stresses, phytoremediation potential and biotic interactions should be a priority given Pongamia's potential to remediate contaminated land and reduce competition for land with edible crops to produce biofuel. Large-scale/long term studies in this context are still lacking and urgently needed so that responses to and mechanisms underlying its tolerances to abiotic stress can be understood in mature trees at different developmental phases. The identification of rhizobia strains and root symbiotic AM fungi which can fulfil Pongamia's nutritional requirements in different contexts is also vital for the successful implementation of large-scale production systems in degraded land and can significantly contribute to its climate change mitigation potential through reductions in fertiliser use. Further understanding of associations between mycorrhizal fungi and Pongamia are also needed, especially outside India, so that it can be included in management strategies. Research on the levels of tolerance to different contaminants, the mechanisms underpinning these, the role of symbiotic association in facilitating the process and the effect it has on tree survival, growth rates, flowering, and yields are vital to ensure that Pongamia plantations can be successfully used as a tool in the regeneration of contaminated land which can benefit not only the environment but also generate socio-economic benefits to communities around these areas. It also important that studies focus on the fate of these contaminants once the oil is processed. Research on agronomic aspects in different contexts are still lacking and this may act as a major adoption barrier both at a small and large scale, especially in Agroforestry systems which have a major potential to contribute to reductions in greenhouse gas emissions and mitigate climate change. Lastly, there should be further efforts to quantify the potential socio-economic benefits of Pongamia, as this will be key to encourage stake holders to invest in the adoption of Pongamia systems.

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Author contribution

MT conceived of the work and was the sole recipient of the supporting grants. ED drafted the manuscript and all authors contributed to portions of writing and critical review. BW and MVRP additionally contributed images and data.

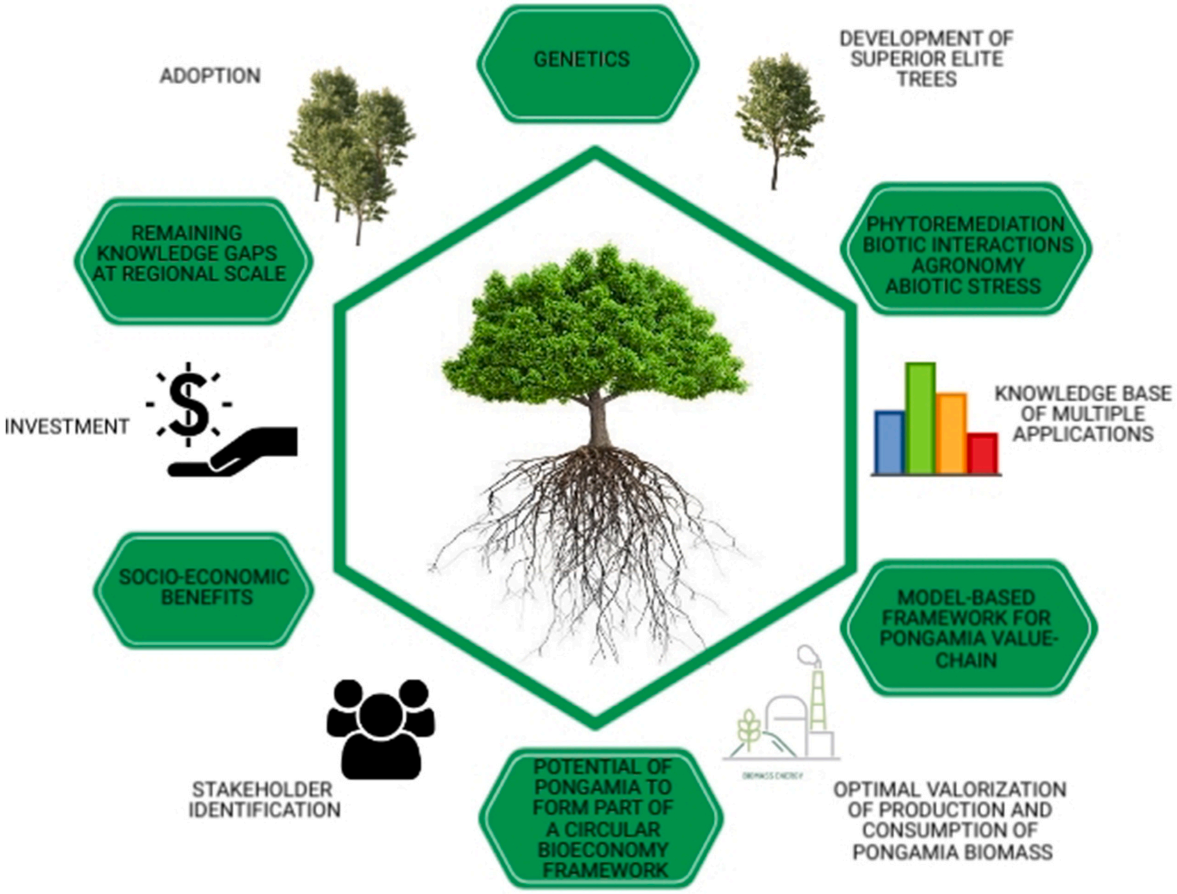

Fig. 6. Suggested Pongamia Research Framework based on findings and recommendations.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests. Benjamin Warr reports a relationship with Phyla Earth that includes: board membership. M.V.R. Prasad reports a relationship with Phyla Earth that includes: consulting or advisory.

Data availability

No data was used for the research described in the article.

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