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REVIEW

Sandalwood: basic biology, tissue culture, and genetic transformation

Jaime A. Teixeira da Silva[1] · Mafatlal M. Kher[2] · Deepak Soner[2] · Tony Page[3] · Xinhua Zhang[4] · M. Nataraj[2] · Guohua Ma[4]

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Abstract

Main conclusion **Sustainable resource preservation of *Santalum* species that yield commercially important forest products is needed. This review provides an understanding of their basic biology, propagation, hemi-parasitic nature, reproductive biology, and biotechnology.**

Many species of the genus *Santalum* (Santalaceae) have been exploited unremittingly for centuries, resulting in the extinction of one and the threatened status of three other species. This reduction in biodiversity of sandalwood has resulted from the commercial exploitation of its oil-rich fragrant heartwood. In a bid to conserve the remaining germplasm, biotechnology provides a feasible, and effective, means of propagating members of this genus. This review provides a detailed understanding of the biological mechanisms underlying the success or failure of traditional propagation, including a synopsis of the process of hemi-parasitism in *S. album*, and of the suitability of host plants to sustain the growth of seedlings and plants under forestry production. For the mass production of economically important metabolites, and to improve uniformity of essential oils, the use of clonal material of similar genetic background for cultivation is important. This review summarizes traditional methods of sandalwood production with complementary and more advanced in vitro technologies to provide a basis for researchers, conservationists and industry to implement sustainable programs of research and development for this revered genus.

Keywords In vitro · Micropropagation · *Santalum album* · *Santalum spicatum* · Somatic embryogenesis · Tissue culture

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✉ Jaime A. Teixeira da Silva
jaimetex@yahoo.com

✉ Mafatlal M. Kher
mafatlalmkher@gmail.com

✉ Deepak Soner
deepaksoner@gmail.com

✉ Tony Page
tpage@usc.edu.au

✉ Xinhua Zhang
xhzhang@scib.ac.cn

✉ M. Nataraj
mnatarajspu@gmail.com

✉ Guohua Ma
magh@scib.ac.cn

[1] P. O. Box 7, Miki-cho Post Office, 3011-2, Ikenobe, Kagawa-ken 761-0799, Japan

[2] B.R. Doshi School of Biosciences, Sardar Patel University, Sardar Patel Maidan, Vadtal Rd., P.O. Box 39, Vallabh Vidyanagar, Gujarat 388120, India

[3] Forests and People Research Centre, University of Sunshine Coast, Maroochydore DC, Locked Bag 4, Sunshine Coast, QLD 4558, Australia

[4] Key Laboratory of Plant Resources Conservation and Sustainable Utilization, South China Botanical Garden, the Chinese Academy of Sciences, Guangzhou 510650, China

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The historical, cultural, medicinal, and economic importance of sandalwood as a basis for conservation

Sandalwood trees of the genus *Santalum* belong to the Santalaceae. This family is composed of 29 genera with approximately 400 species, 19 of which are specific to the *Santalum* genus (Fox 2000; Harbaugh 2007; Harbaugh and Baldwin 2007; Harbaugh et al. 2010; Butaud 2015; Table 1). Encyclopedia Britannica online (2013) lists 36 genera. Harbaugh and Baldwin (2007) placed those numbers as "15 extant species, approximately 14 varieties, and one recently extinct species, distributed throughout India, Australia, and the Pacific Islands." Nageswara Rao et al. (2011) listed 16 species and several varieties. According to The Plant List (2015), currently only 12 species names are accepted, while 41 remain unresolved (Supplementary Table 1). These discrepancies suggest that some attention to the taxonomy of the *Santalum* genus is required.

The economically most prominent species include Indian sandalwood or East Indian sandalwood (*Santalum album* L.), and Australian sandalwood [*S. spicatum* (R.Br.) A.DC.]. Indian sandalwood has various levels of importance in cosmetic, perfumery, and aromatherapy industries, in religion, as well as in traditional medicine (reviewed in Dhanya et al. 2010; Arun Kumar et al. 2012; Heena Kausar et al. 2014). Indian sandalwood was used for carving wooden idols, the manufacture of richly carved boxes, work tables, and cabinets (Chada 1972), and for burning in certain Hindu and Buddhist rituals or to carve deities and temples (Kushalapa 1998). The wood paste was also used as an ointment to dissipate heat (Ral 1990). Sandalwood essential oil, which has a rich tradition of uses spanning more than 4000 years as mentioned in Sanskrit texts, is an important ingredient of cosmetic produces, herbal medicine, and perfumes (Ritter 1836; Burdock and Carabin 2008). The ancient Egyptians imported the wood and used it in medicine, embalming and ritual burning to venerate the gods (Arun Kumar et al. 2012). Historically, sandalwood has a rich tradition of trade with the East, dating as far back as the 5th century BC (Edwards 1951) when its aromatic heartwood and oils were already recognized as prized commodities. Sandalwood trade in India was started as early as the 13th century by Indian rulers trying to monopolize Indian sandalwood resources to ensure economic strength for power and warfare, the classic case being the mighty Vijaya Nagara Empire (13–16 century AC) of the Deccan region (Ganeshaiah et al. 2007). Realizing the value of sandalwood, Tippu Sultan, the King of Mysore (India), declared the sandalwood tree as a royal tree in 1772 (Buchanan 1884; Adkoli 1977). More historical details on Indian sandalwood are available in other reviews (Rai and Sarma 1990; Ganeshaiah et al. 2007; Arun Kumar et al. 2012; Rashkow 2014). Indian sandalwood was extensively exploited in the Pacific throughout the first half of the 19th century although initial evidence of sandalwood trade originated much earlier, with the beginning of Buddhism into China from India (Ritter 1836; Thomson et al. 2005a). This occurred in the first century AD typified by smoldering sandalwood incense in temples. Trade then extended to the Pacific when Americans and Australians began to trade with China, leading to the discovery of sandalwood in the Pacific, including Hawaii, and Australia (Thomson et al. 2005a). Commercial exploitation of sandalwood has, however, resulted in the acute degradation of natural populations of many species, including those in India (Rashkow 2014), Indonesia (Ora 2012), Papua New Guinea (Gunn et al. 2002), and Vanuatu (Gillieson et al. 2008).

Heartwood does not exist in young trees of *S. album* and only mature trees (30–50 years old) produce the heartwood rich in fragrant essential oil (Burdock and Carabin 2008; Zhang et al. 2012b). The concentration of essential oil within the heartwood of mature sandalwood varies between trees, ranging from 0.5 to 5 % in *S. album* (Sindhu Veerendra and Anantha Padmanabha 1996), 0.05–8 % in *S. austrocaledonicum* (Page et al. 2010b), and 0.1–8.2 % in *S. lanceolatum* (Page et al. 2007). Phytochemical analyses of the heartwood of several sandalwood species (*S. album*, *S. spicatum*, *S. austrocaledonicum*, and *S. insulare*) reveal that more than 230 compounds, mainly terpenoids, have been identified so far (reviewed by Baldovini et al. 2011). The Flavor and Extract Manufacturers' Association, the United States Food and Drug Administration, as well as the Council of Europe have approved sandalwood essential oil for use in food-based products (Burdock and Carabin 2008). The essential oils of sandalwood, including bioreactors, will be reviewed separately (Teixeira da Silva et al. unpublished review).

Excessive exploitation of natural stands and the lack of initiatives to establish, until fairly recently, artificial stands has led to a decrease in natural stocks and thus an increase in market prices (Gillieson et al. 2008; Arun Kumar et al. 2012; Subasinghe 2013). Anantha Padmanabha (2000, 2014) described a decline in sandalwood production in India over several decades: 4000 *t* (1950) → 2000 *t* (1990) → ~1000 *t* (1999). More recent figures regarding sandalwood supply in India are difficult to determine, since much of the traded wood comes from illegally harvested sources, and estimates suggest around 1000 tonnes of legally traded wood (AAG 2006; McKinnell 2011). In Indonesia, the sandalwood trade in East Nusa Tenggara Province decreased rapidly during the 1990s contributing almost 50 % of total regional revenue for the early 1990s to

Table 1 *Santalum* species and distribution: modified from Harbaugh and Baldwin (2007), Harbaugh et al. (2010) and Butaud (2015)

Species number	Species	Variety	Distribution
1	*S. album* L		Australia, Indonesia, India
2	*S. austrocaledonicum* Viell.	*austrocaledonicum*	New Caledonia, Vanuatu
		minutum N.Hallé	New Caledonia
		pilosulum N.Halle	New Caledonia
		glabrum Hürl	New Caledonia
3	*S. boninense* (Nakai) Tuyama		Bonin Islands
4	*S. lanceolatum* R.Br.		Australia
5	*S. macgregorii* F.Muell.		Papua New Guinea
6	*S. obtusifolium* R.Br.		Australia
7	*S. yasi* Seem.		Fiji, Tonga
8	*S. freycinetianum* Gaudich.	*freycinetianum*	Hawaiian Islands (O'ahu, Moloka'i)
		lanaiense Rock	Hawaiian Islands (Lana'i, Maui)
		pyrularium (A.Gray) Stemmerm.	Hawaiian Islands (Kaua'i)
9	*S. haleakalae* Hillebr		Hawaiian Islands (Maui)
10	*S. ellipticum* Gaudich.	*ellipticum*	Hawaiian Islands
		littorale (Rock) Skottsb	Hawaiian Islands (O'ahu)
11	*S. paniculatum* Hook. & Arn.	*paniculatum*	Hawaiian Islands (Hawai'i)
		pilgeri (Rock) Stemmerm	Hawaiian Islands (Hawai'i)
12	*S. fernandezianum* F.Phil.		Juan Fernandez Islands[a]
13	*S. insulare* Bertero ex A.DC.	*insulare*	Society Islands (Tahiti)
		alticola Fosberg & Sachet	Society Islands (Tahiti)
		deckeri Fosberg & Sachet	Marquesas Islands
		hendersonense (F.Br.) Fosberg & Sachet	Pitcairn Islands
		marchionense (Skottsb.) Skottsb.	Marquesas Islands
		margaretae (F.Br.) Skottsb.	Austral Islands (Rapa)
		mitiaro Sykes	Cook Islands (Mitiaro)
		raiateense (J.Moore) Fosberg & Sachet	Society Islands (Raiatea, Mo'orea)
		raivavense F.Br.	Austral Islands (Raivavae)
14	*S. acuminatum* (R.Br.) A.DC.		Australia
15	*S. murrayanum* (T.Mitch.) C.A.Gardner		Australia
16	*S. spicatum* (R.Br.) A.DC.		Australia
17	*S. leptocladum* Gand.		Australia
18	*S. involutum* H. St. John		Hawaiian Islands (Kaua'i)

[a] Extinct species

13 % in the late 1990s, and total production continued to decline from 7465 tonnes in the 9 years 1987–1997 to just 2178 tonnes in the 6 years 2001–2007 (Ora 2012).

According to the Tropical Forestry Services, essential oil is extracted from the heartwood of Indian sandalwood by distillation and trades for over $5000/kg on the international market (TFS 2015a). The annual supply of wild-harvested Australian sandalwood species approaches 2000 tonnes of *S. spicatum* (McKinnell 2011), and while a 500 m^3 license exists for *S. lanceolatum* (DPI&F 2004; Timber-Queensland 2012), others suggests that actual annual yields fluctuate between 120 and 400 tonnes [equivalent to between 49.86 and 166.21 m^3; conversion using Traditionaloven.com (2015)]; (AAG 2006; McKinnell 2011). The average auction price for the heartwood of wild Indian sandalwood rose from $9,400/tonne in 1990 (Ral 1990) to approximately $150,000/tonne in July 2014 (on small volumes based on an auction held in Tamilnadu, India), which indicates a significant annual compounded growth rate (TFS 2015b). A 12 % annual increase in the minimum price paid to landowners for *S. austrocaledonicum* in Vanuatu has also been recorded, from an equivalent of US$4/kg in 2000 (Mele 2001; Berry 2005) to US$20/kg in 2015 (Tosul 2015). The price of *S. spicatum* varies considerably between product grades, and in 2007–2008, export prices ranged from USD 3000 to

10,000/tonne (McKinnell 2011), which has increased to USD 8000 to 17,000/tonne in 2014–2015 (Zauba.com 2015). The price of Indian sandalwood is ten times higher than that of Australian sandalwood while the heartwood of Indian sandalwood yields more essential oil with a higher proportion of α- and β-santalols—important constituents of sandalwood oil fragrance—than other sandalwood species (Baldovini et al. 2011; FAO 2015; TFS 2015a). This positive economic perspective makes Indian sandalwood an attractive option for commercial growers aiming at international perfumery, cosmetic, and pharmaceutical markets (Christian 2015).

Indian sandalwood tree is a hemi-parasitic plant that requires a host for sustained growth (discussed in more detail in the section "Hemi-parasitism and host plant dependence"), making cultivation practices highly specialized. These factors, together with its strong demand in Asia and the Middle East for the global fragrance industry, have led to the mass deforestation of Indian sandalwood from natural habitats. Indian sandalwood was first classified as vulnerable by the International Union for Conservation of Nature (IUCN) in 1998 (IUCN 2015a). The Convention on International Trade in Endangered Species (CITES) also considers closely related *S. austrocaledonicum*, *S. yasi*, and *S. insulare* as endangered (CITES 2013). Four *Santalum* species, namely *S. album* (vulnerable due to factors like fire, grazing, exploitation of wood and smuggling; IUCN 2015a), *S. fernandezianum* (extinct due to cutting for the aromatic wood; IUCN 2015b), *S. macgregorii* (endangered due to overexploitation of the scented wood for incense; IUCN 2015c), and *S. haleakalae* (vulnerable; IUCN 2015d), are listed in the IUCN Red Data List. The use of traditional technologies such as seed germination, as well as the use of applied biotechnologies, such as tissue culture, would allow production to be standardized, and perhaps even reverse species decline through the production of cultivated stands.

In southern China, great efforts are being made to increase production (Zhang et al. 2007) while plantations have expanded in India, China, Indonesia, and Australia over the past 20 years (Dhanya et al. 2010; Lu 2011). Indian sandalwood (*S. album*) plantings in Australia are currently approaching 11,000 ha with two main producers Tropical Forestry Services (TFS 2015c) having just over 9000 hectares and Santanol who acquired Elders Forestry estate in 2013 (Jackman 2013) comprising approximately 1800 ha (Werren 2011). In South China, plantation of *S. album* on a large scale began in 2013 increasing rapidly to 5000 ha, planted mainly in mountain areas (Guohua Ma, unpublished data). According to Western Australian Forest Products Commision (FPC), the 2015 Australian sandalwood (*S. spicatum*) plantings in Australia are approaching 20,000 ha (Erasmus (General Manager of FPC) pers. comm. 2015). Planted sandalwood in Vanautu (*S. austrocaledonicum*) comprises largely small-scale woodlots with an estimated area of approximately 550 ha planted by 2006 with planting continuing to date (Page et al. 2010a).

This review aims to explore the basic biology and propagation of the genus *Santalum*, how in vitro tissue culture has been used to produce clonal plant material, and what promises this technology holds in aiding the conservation and mass propagation of threatened *Santalum* germplasm.

Basic biology and propagation

Basic biology, flowering control, reproductive mechanisms, and breeding

Sexual reproduction

The onset of reproductive maturity in several sandalwood species (*S. album*, *S. austrocaledonicum*, *S. macgregorii*, *S. spicatum*, and *S. yasi*) occurs between 2 and 5 years (Jiko 1993; Barrett and Fox 1995; Doran and Brophy 2005). Sexual reproduction in sandalwood may be considered to be opportunistic with several species flowering across most months of the year, with two (sometimes three) peak periods following favorable rainfall events/periods. In *S. austrocaledonicum* (Doran and Brophy 2005), *S. macgregorii* (Bosimbi 2005), and *S. yasi* (Bulai and Nataniela 2005), a low level of reproduction may be found across most months of the year. The periods of peak fruit production occur in both wet and dry seasons with the most prominent of these two peaks occurring in the wet months for *S. album* (in India and Timor) (Suriamihardja and Suriamihardja 1993) and *S. yasi* (in Fiji) (Bulai and Nataniela 2005) and the dry months for *S. austrocaledonicum* (in Vanuatu) (Daruhi 1993; Doran and Brophy 2005). Reproduction in *S. spicatum* (Applegate et al. 1990; Loneragan 1990) and *S. lanceolatum* (Applegate and McKinnell 1993) is highly dependent upon rainfall events, and the timing and location of seed crops are highly variable. The period of fruit development in tropical sandalwood species typically occurs over a 2- to 3-month period (Corrigan et al. 2005), whereas it can take up to 6 months for the fruit to mature in *S. spicatum* (Barrett and Fox 1995).

The general breeding system of *Santalum* species may be described as facultatively allogamous (incompletely outbreeding), with variation between families and individuals at the level of self-incompatibility (Ma et al. 2006; Muir et al. 2007; Tamla et al. 2011) and with no capacity for apomixis or parthenocarpy (Ma et al. 2006; Tamla et al.

2011). The preferential outcrossing nature of the breeding system and the capacity for self-fertilization is advantageous, providing the genus a capacity to colonize new islands.

Across all sandalwood species studied, only a low proportion of controlled cross-pollinated flowers successfully develop into mature seed. The proportions range from 1.3 % in *S. spicatum* (Rugkhla et al. 1997), 7.5 % in *S. lanceolatum* (Tamla et al. 2011), and 9.4–14 % in *S. album* (Rugkhla et al. 1997; Kulkarni and Muniyamma 1998; Ma et al. 2006). Percent seed set in *S. album* following open-pollination was 2–5.2 % (Sindhu Veerendra and Anantha Padmanabha 1996; Ma et al. 2006), which was lower than that reported for controlled cross-pollination (9.4–14 %). The low percentage seed set in sandalwood can therefore be influenced by the effectiveness of pollen vectors to influence successful cross-pollination.

Sandalwood species are largely pollinated by a diverse range of insect vectors (Sindhu Veerendra and Anantha Padmanabha 1996; Kulkarni and Muniyamma 1998; Tassin 2005) including bees (Apidae, Xylocopidae, Anthorphoridae), ants (Formicidae), wasps (Eumeninae, Vespidae and Sphecidae), flies (Sarcophagidae, Calliphoridae, Muscidae and Syrphidae), and moths and butterflies (Danaidae, Pieridae and Papilionidae) (Jyothi et al. 1991; Bhaskar 1992; Baskorowati 2011; Ratnaningrum and Indrioko 2014). Ratnaningrum and Indrioko (2014) found that bees were the most frequent flower visitors in *S. album*, followed by ants, butterflies, moths, wasps, and flies. Insect visitors to *S. album* flowers were found to be most prevalent in the morning (Baskorowati 2011) in the following sequence: moths (06:00–08:00), bees (07:00–10:00), wasps (08:00–10:00), and butterflies (09:00–12:00), while ants and flies were observed tending flowers throughout the day (Ratnaningrum and Indrioko 2014).

This aspect of sandalwood reproductive biology is an important consideration for the conservation of wild stands, since the distribution structure and density of reproductively mature trees is likely to influence cross-pollination, seed set, and potential seedling recruitment.

While effective cross-pollination is an important factor influencing seed set in sandalwood, substantial abscission of immature fruit (75–80 % fruit drop) can be found in *S. album* and *S. spicatum* following controlled outcross pollination (Rugkhla et al. 1997). Given that these authors found 10–40 % of cross-pollinated flowers had evidence of successful fertilization, it is possible that the abscission of immature fruit can be caused by maternal resource limitation when pollination is not a limiting factor. *Santalum* species can therefore be described as mass-flowering with typically less than 10 % developing into viable seed.

Self-incompatibility

The sandalwood species *S. album* and *S. spicatum* have been recorded to have self-incompatibility mechanisms operating at both pre- and post-fertilization (Rugkhla et al. 1997). In *S. lanceolatum*, Warburton (2000) found evidence of self-incompatibility or pistil dysfunction and Tamla et al. (2011) identified possible self-incompatibility. Given that *S. album*, *S. lanceolatum*, and *S. spicatum* occupy distinct phylogenetic clades (Harbaugh and Baldwin 2007), it is possible that self-incompatibility is widespread within the genus.

Genetic variation in the expression of self-incompatibility in sandalwood is likely, with 20 % of *S. lanceolatum* demonstrating 'self' fertility (Tamla et al. 2011), Muir et al. (2007) finding a high level of inbreeding within one family of *S. spicatum*, and Ma et al. (2006) reporting that 24 % of self-pollinated flowers set seed in *S. album*. This flexibility in breeding strategy would be of advantage in continental Australian species dispersing and colonizing many islands in south-east Asia and Pacific (Harbaugh and Baldwin 2007).

Interspecific incompatibility/hybridization

The development of viable hybrid progeny has been reported for crosses between *S. album* with each of *S. austrocaledonicum* (Tamla et al. 2011), *S. lanceolatum* (Tamla et al. 2011), and *S. yasi* (Bulai and Nataniela 2005; Doran et al. 2005) despite total geographic isolation and substantial morphological variation between them.

A phylogenetic study of the genus *Santalum* using nuclear ribosomal and chloroplast DNA sequences revealed that the earliest genetic divergence was of *S. acuminatum* and *S. spicatum* splitting from all remaining lineages (Harbaugh and Baldwin 2007). This early divergence of *S. spicatum* reflects a relatively distant genetic relationship with *S. album* and incongruity between their mating systems (Rugkhla et al. 1997). This incongruity can be observed as an incompatibility mechanism between pollen and style, and possibly within the developing zygote (Rugkhla et al. 1997).

The phylogenetic clade containing the species *S. austrocaledonicum* and *S. lanceolatum* (sensu stricto) was found to diverge from the clade containing *S. album* and *S. yasi* between 6.3 and 9.5 million years ago (Harbaugh and Baldwin 2007). Given that no clear reproductive barriers exist between all four of these species (Tamla et al. 2011), it is possible that no further divergence of these species' breeding system has occurred during that time. Given that these two clades comprise 12 of the 15 extant *Santalum* species (Harbaugh and Baldwin 2007), it may be possible that hybridization between species is the norm rather than

the exception in this genus. This feature of the breeding system can facilitate the introgression of traits between species and the development of hybrids. Introduction of exotic sandalwood species within the natural range of a compatible species will likely result in uncontrolled gene flow between them and modify the genetic structure and diversity of the local species.

Karyological studies in sandalwood

Karyological studies are a prerequisite for the creation of innovative new varieties in plant genetics and breeding. Polyploidy is widely acknowledged as one form of breeding in plants. Previous studies showed that the somatic cells of *Santalum* were diploid, with $2n = 20$, including *S. album* (Rao 1942b), *S. ellipticum*, *S. freycinetianum*, and *S. paniculatum* (Carr 1978). Forty chromosomes were observed in many haustorium cells of *S. album* (Srimathi and Sreenivasaya 1962). Harbaugh (2008) reported four ploidy levels in *Santalum* ranging from diploid ($n = 10$) to octoploid ($n = 40$) based on flow cytometric analysis of DNA content of 16 *Santalum* species and 5 varieties across Pacific islands (*S. album*, *S. yasi*, *S. spicatum*, *S. paniculatum*, *S. obtusifolium*, *S. murrayanum*, *S. macgregorii*, *S. leptocladum*, *S. lanceolatum*, *S. haleakalae*, *S. insulare* var. *marchionense*, *S. insulare* var. *raiateense*, *S. freycinetianum* var. *freycinetianum*, *S. freycinetianum* var. *lanaiense*, *S. freycinetianum* var. *pyrularium*, *S. ellipticum* var. *ellipticum*, *S. ellipticum* var. *littorale*, *S. boninense*, *S. austrocaledonicum*, and *S. acuminatum*) (Harbaugh 2008), the majority of which were diploid and tetraploid, with $2n = 20$ and $2n = 40$, respectively. The results from this study suggest that two allopolyploid events between distantly related species and four putatively autopolyploid events occurred in *Santalum*, indicating that the *Santalum* island colonists have a tendency to be polyploid. Polyploids in *Santalum* are likely to be better suited than diploids for long-distance dispersal and successful establishment on oceanic islands, since polyploidy may increase the likelihood of their establishment and long-term survival across the Pacific islands by decreasing inbreeding depression (Harbaugh 2008).

A detailed karyomorphological study on *S. album* revealed that the interphase nucleus was a simple chromocenter type while the prophase chromosomes were of the interstitial type (Zhang et al. 2010). A mixoploid of $2n = 2x = 20$ and $2n = 4x = 40$ was found in the shoot-tip meristem cells of some *S. album* individuals, of which about 5 % was found to be tetraploid ($4n = 40$). The karyotypic formulae analyzed showed that centromeres were predominantly in a median position with a few submedian centromeres, i.e., $2n = 20 = 18\ m + 2sm$ and $2n = 40 = 32\ m\ (2SAT) + 8sm$, respectively. The karyotypes belonged to the 2B type of Stebbins' karyotypic symmetry (Stebbins 1971), suggesting that *S. album* was a primitive taxon. Somatic cells of *S. yasi* and the spontaneous F1 hybrid, *S. album* × *S. yasi*, were diploid, with $2n = 20$ (Zhang et al. unpublished data). These results allow species and this hybrid in *Santalum* to be exploited and utilized in future plant breeding programs.

Propagation

Seed propagation

Seeds are important organs of higher plants since they contain the zygotic embryo, a vital part of the reproductive life cycle that is renewed when seeds are dispersed followed by seed germination. The seeds of many sandalwood species are naturally dispersed by bird-based endozoochory (Batabyal et al. 2014). In contrast, the seeds of *S. spicatum* are dispersed by a small marsupial known as a woylie (Murphy et al. 2005). Seed can be induced to germinate artificially under controlled environmental conditions, but this depends on the stage of fruit development and even on the source and size of seed (Manonmani and Vanangamudi 2002), usually after breaking dormancy (Jayawardena et al. 2015). Manonmani and Vanangamudi (2001) noted that black fruits (most mature) showed a higher germination percentage than brown or red fruits (73.2, 68.2, and 29.0 %, respectively). However, Hirano (1990) showed that simple removal of the testa, and a dip of naked seed in Dithane™ M45 (a fungicide) for 5 min, could result in 67 % germination for Indonesian *S. album*, 26 days to germination and seed viability of 324 days (assessed by the total number of days between first and last seedling). These values, also in Hirano's study, were 77 %, 75 and 824 days for *S. paniculatum*, and 38 %, 155 and 387 days for *S. haleakalae*; these species originate from Hawai'i. Hirano (1990) used a substrate consisting of vermiculite, perlite, and peat plus osmocote (18-6-12) (2:2:1), noting that chelated iron (Sequestrene 138 Fe) was essential for seed germination and seedling growth. *S. album* seeds germinated more rapidly when the testa was removed, and seeds were soaked in 0.05 % gibberellic acid (GA_3) for 12–16 h (Nagaveni and Srimathi 1981; Das and Tah 2013). A similar treatment was suggested for *S. macgregorii* seed germination by Gunn et al. (2002). Gamage et al. (2010) reported that the germination efficacy of stored *S. album* seeds decreases over time, reaching 0 % after 28th weeks, suggesting that seeds should be sown once shed rather than using stored seeds and that germination trials should be started early (Gamage et al. 2010). Seed germination of *S. spicatum* in natural conditions is very poor, and only 1–5 % seeds germinate (Loneragan 1990). Liu et al. (2009) found that a substrate mixture of burnt soil, peat, and

coconut dust (1:1:1, w/w), including 2 % calcium superphosphate, resulted in 98 % survival (as well as greater height and biomass than other substrates) of *S. album* seedlings when *Kuhnia rosmarinifolia* Vent. was used as the primary host plant and after treating surface-sterilized (0.1 % mercuric chloride for 5–6 min and three washes in distilled water) seeds with 1 mg/L GA_3 for 24 h. Lu et al. (2013) soaked *S. album* seeds in 0.1 % GA_3 for 12 h using the protocol of Radomiljac (1998) then surface-sterilized them with 3 % NaOCl for 5 min, washed them with distilled water, and then germinated them on sterilized sand soaked with distilled water at 28–30 °C for 3–4 weeks. When germination conditions are suitable and in association with an appropriate host, this method can be useful for the large-scale seed germination of *S. album* (Ral 1990), as summarized in Fig. 1 (specific for Karnataka, India). Athelstone et al. (1994) assessed the effects of plant growth regulators (ethrel, silver thiosulfate, 6-benzyladenine, kinetin, GA_3, and GA_4) on *S. accuminatum* seed germination. They found that cracking seed and treatment with 580 µM GA_3 (duration of treatment not reported) resulted in 90 % seed germination within 43 days. Jayawardena et al. (2015) found that scarification and 500 mg/L GA_3 could increase germination to 100 % from near-zero levels in non-scarified control *S. album* seeds. Chauvin and Ehrhart (1998) observed differences in germination rates of two provenances of *S. austrocaledonicum* var. *austrocaledonicum*: 55 % germination in the "Ile des Pins" provenance after 2 years and 0 % germination in the "Mare" provenance with the exception of 19 % germination in one lot after 15 months. Nasi (1995) had noted that 25 % germination of *S. austrocaledonicum* var. *pilosulum* was possible without pre-treatment, but only after 1 year; however, removing the endocarp, nicking the seeds, not storing seeds, and soaking seeds in 100 mg/L GA_3 all increased the germination percentage at 28 °C. Natural stands of *S. album* growing in East Nusa Tenggara Province in Indonesia showed regeneration percentages ranging widely from 4.85 to 48.4 % (Wawo 2008).

In vivo or in vitro germinated seedlings can be used as ideal rootstock for grafting (Sanjaya and Rai 2003). Sanjaya et al. (2006a) managed to attain a 50 % in vivo micrografting rate of success in *S. album* when 4- to 5-cm-long scions, collected from a candidate plus tree (CPT) of 50–60 years of age, were grafted onto 90-day-old nursery-grown rootstock. Sanjaya et al. (2006a) reported that scion size, rootstock age, and scion collection season are vital factors that affect graft success. Grafted plants were kept under greenhouse conditions for 6–8 weeks to allow for graft union. In vitro micrografts were accomplished by placing 1- to 2-cm-long scions collected from nodal cuttings (obtained from CPT) onto the hypocotyl of 45-day-old in vitro rootstocks. The use of in vitro-grown shoots as a source of scions improved graft success (60 %) more than scions obtained directly from field-grown trees. The success rate of in vitro grafting was also affected by scion size and rootstock age. Under suitable conditions, scions and hypocotyls united to form complete plants with 2–4 leaves within 6–8 weeks (Sanjaya et al. 2006a). Grafting of *S. austrocaledonicum* has also been demonstrated using a top-wedge graft with actively growing semi-hardwood stems (Tate et al. 2006). These authors suggested that the success of grafting was dependent upon the skill of the propagator with the percentage of successfully grafted unions varying between 60 and 90 %.

Thus, techniques for the establishment of a seedling stock are well established, although mechanization of the process is less explored. To address this gap, St. Jack et al. (2013) devised a seed metering device that would optimize the mechanization of seed planting and germination.

Vegetative propagation

Various authors have reported on successful vegetative propagation of *S. album* by cuttings. Uniyal et al. (1985) demonstrated that *S. album* can be propagated by root cuttings with 60 % success when they used Seradix B2® at the time of planting during the first week of April under Indian conditions. *S. lanceolatum* can be propagated by root suckers (Warburton et al. 2000). Havea (2012) reported that *S. yasi*, *S. album*, and their hybrids can be vegetatively propagated using apical cuttings from younger seedlings (up to 12 months of age). They recommended treating the cuttings with indole-3-butyric acid and α-naphthaleneacetic acid (1.0 mg/L each) and using a substrate composed of sand:peatmoss (30:70, w/v).

Batabyal et al. (2014) proposed that *S. album* can be propagated using 15-cm-long stem cuttings from 3- to 4-year-old trees by treatment with 1.5 mg/L indole-3-acetic acid (IAA) and 1.5 mg/L GA_3, resulting in most leaves per branch, although rooting percentages among the treatments were not reported. These authors were also able to increase the number of branches per cutting by applying 1.5 mg/L IBA and kinetin. Rao and Srimathi (1977) attempted air layering to clonally propagate *S. album*, in which branches of 2 cm thick from different seasons' growth were used, observing that March–April (rainy season) were most favorable for air layering under Indian conditions. Collins et al. (2000) found substantial variation in the percentage of stem cuttings with adventitious roots between experiments, genotypes and species. Differences between experiments were recorded for *S. album* (9.5 and 0 % rooting), *S. austrocaledonicum* (63.5 and 20.2 %), and *S. yasi* (46.1 and 10.1 %). Differences were observed between 15 *S. austrocaledonicum* genotypes with root induction ranging from 25 to 88.9 %. It has been proposed

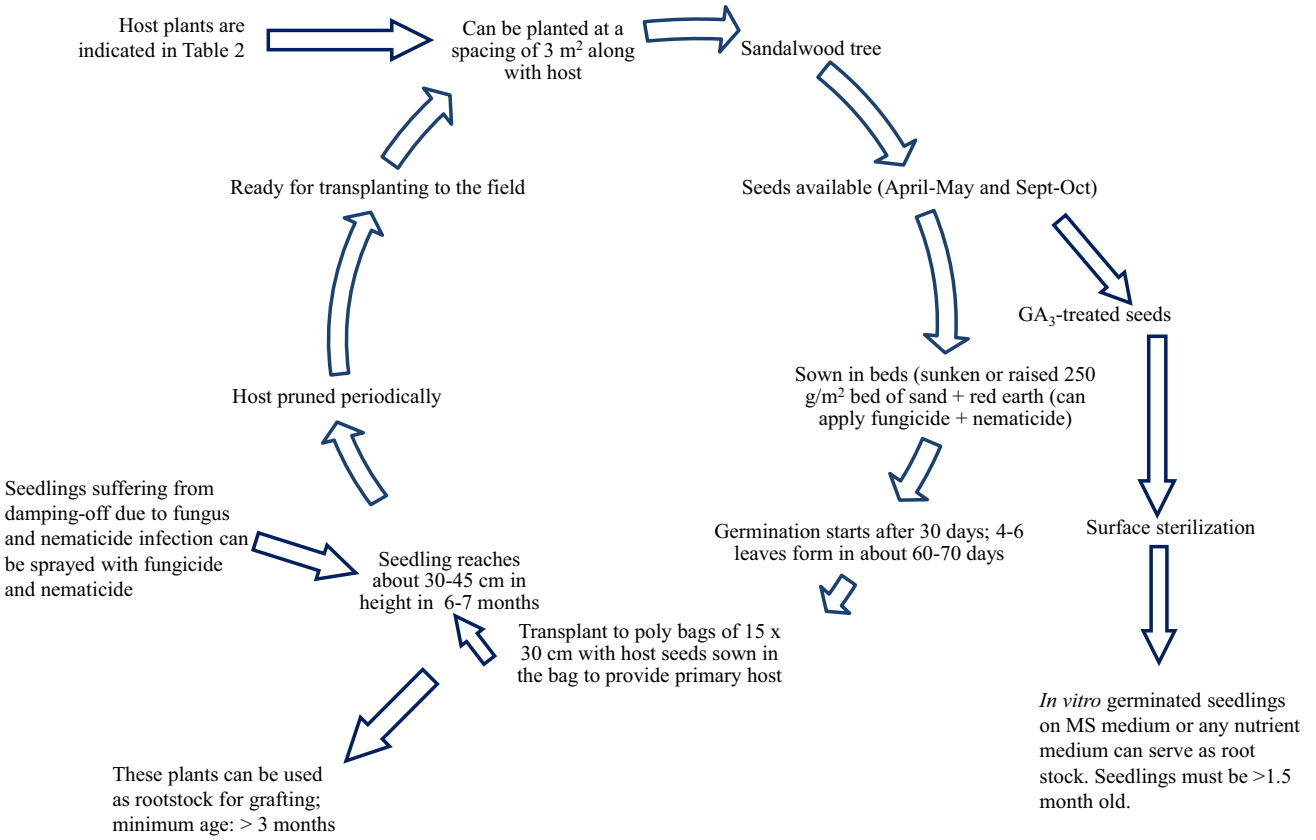

Fig. 1 Cultivation of sandalwood from seeds (modified from Ral 1990)

that *S. yasi* and *S. austrocaledonicum* are more amenable to stem cutting propagation than *S. album*, *S. lanceolatum*, and *S. macgregorii* (Collins et al. 2000; Thomson et al. 2005b). The differences observed in the series of experiments conducted by Collins et al. (2000) indicate that it is difficult to generalize the optimum conditions required for successful stem cutting propagation across the *Santalum* genus.

Hemi-parasitism and host plant dependence

First noted by Scott (1871), and further confirmed by Brandis (1903), *Santalum* species are hemi-parasitic, whereby they derive part of their water and nutrient requirements from a host plant. Under cultivation, sandalwood species require hosts during all stages of production including the pot stages, in the first years of establishment and at maturity (Ehrhart and Fox 1995; Fox et al. 1996; Radomiljac et al. 1998a, 1999a; Annapurna et al. 2006), although the choice of potting medium can also be an influencing factor (Annapurna et al. 2005). Sandalwood can potentially be grown across a range of environments provided locally adapted host species can be identified for each stage of cultivation (Table 2). Among these families, many species of the Fabaceae, Mimosaceae, Casuarinaceae, Meliaceae, Myrtaceae, Apocynaceae, and Rhamnaceae are proven good hosts. However, not all species in these families are good hosts. For example, in the Fabaceae, many species, including *Butea monosperma* and *Tamarindus indica*, are poor hosts (Table 2).

Annapurna et al. (2004) noticed that the container size for potting influenced the success of pot growth, with 600 ml pots being an ideal size for *S. album* seedlings, producing plantlets 20 cm high within 6 months when in the presence of pigeon pea [*Cajanus cajan* (L.) Millsp.] as the host plant. These authors also recommended a potting mixture of sand, soil, compost, burnt rice husk, and charcoal (5:3:10:1:1). Despite these optimized conditions, the authors noted that root development was quite poor, indicating that one possible reason might be the use of an inappropriate host. Radomiljac (1998) had previously used *Alternanthera nana* R.Br. and *Sesbania formosa* (F. Muell.) N. Burb. as the primary host in pot experiments that used 1500 ml pots in a substrate consisting of sand, peat, and perlite (3:2:2), successfully increasing the survival, height, and diameter of *S. album* plants; in that study, *Atalaya hemiglauca* (F.Muell.) F.Muell. ex Benth, *Acacia hemignosta* F.Muell, and *Crotalaria retusa* L. were not

Table 2 Host plants (suitable and unsuitable) for sandalwood (chronological listing)

Species	Country of test	Suitable hosts	Family	Unsuitable hosts	Family	References
S. album	India	*Azadirachta indica* A.Juss	Meliaceae	*Butea monosperma* (Lam.) Taub.	Fabaceae	Parthasarathi et al. (1974)
		Cassia fistula L.	Fabaceae	*Dodonea viscosa* Jacq.	Sapindaceae	
		C. siamea (Lam.) lrwin et Barneby	Fabaceae	*Gmelina arborea* Roxb.	Lamiaceae	
		Dalbergia latifolia Roxb.	Fabaceae	*Melia azedarach* L.	Meliaceae	
		Ficus bengalensis L.	Moraceae	*Tamarindus indica* L.	Fabaceae	
		Grevillea robusta A.Cunn. ex R.Br.	Proteaceae			
		Pithecellobium dulce (Roxb.) Benth.	Fabaceae			
		Pongamia pinnata (L.) Panigrahi	Fabaceae			
		Syzygium cumini (L.) Skeels.	Myrtaceae			
		Wrightia tinctoria (Roxb.) R.Br.	Apocynaceae			
		Zizyphus mauritiana Lam.	Rhamnaceae			
S. spicatum	Australia	*Acacia acuminata* Benth.	Mimosaceae	NR		Struthers et al. (1986)
S. album	India	*Acacia nilotica* (L.) P.J.H.Hurter & Mabb.	Fabaceae	NR		Anantha padmanabha et al. (1988)
		Bauhinia biloba L.	Fabaceae			
		Cassia siamea (Lam.) Lrwin et Barneby	Fabaceae			
		Casuarina equisetifolia L.	Casuarinaceae			
		Dalbergia sissoo Roxb.	Fabaceae			
		Melia dubia Cav.	Meliaceae			
		Pongamia pinnata (L.) Panigrahi	Fabaceae			
		Terminalia arjuna (Roxb.) Wight & Arn.	Combretaceae			
		T. alata Heyne ex Roth	Combretaceae			
		Wrightia tinctoria (Roxb.) R.Br.	Apocynaceaea			
S. acuminatum	Australia	*Acacia rostellifera* Benth.	Mimosaceae	*Melaleuca viminea* Lindl.	Myrtaceae	Tennakoon et al. (1997)
		A. pulchella R. Br.	Mimosaceae			
		Allocasuarina campestris (Diels) L. Johnson	Casuarinaceae			

Table 2 continued

Species	Country of test	Suitable hosts	Family	Unsuitable hosts	Family	References
S. acuminatum	Australia	*Acacia rostellifera* Benth.	Mimosaceae	NR		Tennakoon et al. (1997b)
		A. pulchella R. Br.	Mimosaceae			
		Allocasuarina campestris (Diels) L. Johnson	Casuarinaceae			
		Alyogyne hakeaefolia (Giord.) Alef.	Malvaceae			
		Anthocercis viscosa R. Br.	Solanaceae			
		Baeckea tetragona Benth.	Myrtaceae			
		Cryptandra mutila Reisseck.	Rhamnaceae			
		Dodonaea aptera Miq.	Sapindaceae			
		Exocarpos sparteus R. Br.	Santalaceae			
		Leucopogon ovalifolius Sonder.	Epacridaceae			
		Lysinema ciliatum R. Br.	Epacridaceae			
		Melaleuca viminea Lindley	Myrtaceae			
		Spyridium cordatum (Turca.) Benth.	Rhamnaceae			
S. spicatum	Australia	*Acacia acuminata* Benth.	Fabaceae	*Allocasuarina huegeliana* (Miq.) L.A.S. Johnson	Casuarinaceae	Brand et al. (1998, 2000, 2003); Brand (2009)
				Eucalyptus loxophleba subsp. *loxophleba*	Myrtaceae	
S. album	Australia	*Acacia* trachycarpa E. Pritzal	Mimosaceae	*Eucalyptus camaldulensis* Dehnh.	Myrtaceae	Radomiljac et al. (1998b, 1999a,b,c)
		A. ampliceps Maslin.	Mimosaceae			
		Sesbania formosa (F. Muell) N. Burb.	Papilionaceae			
S. acuminatum	Australia	*Melia azedarach* L.	Meliaceae	NR		Loveys et al. (2001a)
		Myoporum parvifolium R.Br.	Scrophulariaceae			
S. acuminatum	Australia	*Acacia pycnantha* Benth.	Mimosaceae	*Eucalyptus fasciculosa* F. Mueller	Myrtaceae	Loveys et al. (2001b)
		Atriplex vesicaria Benth.	Amaranthaceae	*Eucalyptus camaldulensis* Dehnh.	Myrtaceae	
		Heterodendrum oleifolium Desf.	Sapindaceae			
		Pittosporum phylliraeoides DC.	Pittosporaceae			
		Rhagodia spinescens var. *deltaphylla*	Amaranthaceae			
S. acuminatum	Australia	*Acacia cyclops* A Cunn. Ex G. Don	Mimosaceae	NR		Loveys et al. (2002)
		Atriplex nummularia Lindl.	Amaranthaceae			
		Myoporum parvifolium R. Br.	Scrophulariaceae			
		Templetonia retusa (Vent.) R. Br.	Fabaceae			
S. acuminatum	Australia	*Acacia acuminata* Benth.	Mimosaceae	NR		Woodall and Robinson (2002)

Table 2 continued

Species	Country of test	Suitable hosts	Family	Unsuitable hosts	Family	References
S. acuminatum	Australia	*Acacia acuminata* Benth.	Mimosaceae	*Acacia cyclops* A.Cunn. ex G. Don	Mimosaceae	Woodall and Robinson (2003)
		A. asepala Maslin	Mimosaceae	*A. jibberdingensis* Maiden & Blakely	Mimosaceae	
		A. assimilis S.Moore	Mimosaceae	*Alyxia buxifolia* R.Br.	Apocynaceae	
		A. cochlearis (Labill.) H.L.Wendl.	Mimosaceae	*Astroloma prostratum* R.Br.	Epacridaceae	
		A. declinata R.S. Cowan & Maslin	Mimosaceae	*A. epacridis* (DC.) Druce	Epacridaceae	
		A. erinacea Benth.	Mimosaceae	*Dichopogon fimbriatus* (R.Br.) J.F.Macbr.	Anthericaceae	
		A. glaucoptera Benth.	Mimosaceae	*Dryandra armata* R.Br.	Proteaceae	
		A. lasiocalyx C.R.P.Andrews	Mimosaceae	*Enchylaena tomentosa* R.Br.	Chenopodiaceae	
		A. microbotrya Benth.	Mimosaceae	*Eucalyptus perangusta* Brooker	Myrtaceae	
		A. patagiata R.S. Cowan & Maslin	Mimosaceae	*E. salmonophloia* F.Muell.	Myrtaceae	
		A. pulviniformis Maiden & Blakely	Mimosaceae	*E. tetragona* (R.Br.) F.Muell	Myrtaceae	
		A. saligna H. Wendl.	Mimosaceae	*Grevillea nudiflora* Meisn.	Proteaceae	
		A. sulcata R.Br.	Mimosaceae	*Hybanthus floribundus* (Lindl.) F.Muell.	violaceae	
		Allocasuarina campestris (Diels) L.A.S.Johnson	Casuarinaceae	*Melaleuca pentagona* Labill.	Myrtaceae	
		A. huegeliana (Miq.) L.A.S.Johnson	Casuarinaceae	*Nemcia hookeri* (Meisn.) Crisp	Papilionaceae	
		A. humilis (Otto & F.Dietr.) L.A.S.Johnson	Casuarinaceae	*Opercularia spermaocea*	Rubiaceae	
		A. microstachya (Miq.) L.A.S.Johnson	Casuarinaceae	*Oxylobium microphyllum* Benth.	Papilionaceae	
		A. thuyoides (Miq.) L.A.S.Johnson	Casuarinaceae	*Petrophile fastigiata* R.Br.	Proteaceae	
		Banksia attenuate R.Br.	Proteaceae	*P. seminuda* Lindl.	Proteaceae	
		Dampiera lavandulacea Lindl.	Goodeniaceae	*Rhagodia baccata* (Labill.) Moq.	Henopodiaceae	
		Daviesia incrassate Sm.	Papilionaceae	*Spyridium majoranifolium* (Fenzl) Rye	Rhamnaceae	
		D. teretifolia Benth.	Papilionaceae	*Synaphea petiolaris* R.Br.	Proteaceae	
		Dodonaea humifusa Miq.	Sapindaceae			
		D. ptarmicaefolia Turcz.	Sapindaceae			
		Gastrolobium parviflorum (Benth.) Crisp	Papilionaceae			
		Hakea lissocarpha R.Br.	Proteaceae			
		H. nitida R.Br.	Proteaceae			
		H. preissii Meisn.	Proteaceae			
		H. trifurcata (Sm.) R. Br.	Proteaceae			
		Halgania cyanea Lindl.	Boraginaceae			
		Hibbertia rupicola (S.Moore) C.A.Gardner	Dilleniaceae			
		Jacksonia furcellata (Bonpl.) DC.	Papilionaceae			
		Labichea lanceolata Benth.	Caesalpiniaceae			

Table 2 continued

Species	Country of test	Suitable hosts	Family	Unsuitable hosts	Family	References
		Lasiopetalum rosmarinifolium (Turcz.) Benth.	Sterculiaceae			
		Olearia axillaris (DC.) Benth.	Asteraceae			
		O. muelleri Benth.	Asteraceae			
		Senna artemisioides subsp. *filifolia* Randell	Caesalpiniaceae			
		Templetonia retusa (Vent.) R. Br.	Papilionaceae			
		Thomasia angustifolia Steud.	Sterculiaceae			
S. album	India	*Azadirachta indica* A. Juss	Meliaceae	*Artocarpus integrifolia* L.	Moraceae	Nagaveni and Vijayalakshmi (2003)
		Cajanus cajan (L.) Millsp.	Papilionaceae	*Acacia auriculiformis* A. Cunn. Ex Benth.	Fabaceae	
		Casuarina equisetifolia L.	Casuarinaceae	*Swietenia mahogani* L.	Meliaceae	
		Eucalyptus camaldulensis Dehnh.	Myrtaceae			
		Pongamia pinnata L.	Fabaceae			
		Tectona grandis L.	Verbenaceae			
		Wrightia tinctoria (Roxb.)R.Br.	Apocynaceae			
S. album	China	*Acacia auriculaeformis* A. Cunn.	Fabaceae	*Artocarpus heterophyllus* (Wall.) R. N. Park.	Moraceae	Li (2003)
		Acacia confusa Merr.	Fabaceae	*Camellia odorata* Abel.	Theaceae	
		Albizia lebbek (L.) Benth.	Fabaceae	*Mangifera indica* Linn	Anacardiaceae	
		Caesalpinia pulcherrima L.	Caesalpiniaceae	*Ormosia fordiana* Oliv.	Papilionaceae	
		Casuarina junghuhniana Miq.	Casuarinaceae	*Pterocarpus echinatus* Pers.	Fabaceae	
		Cajanus cajan (L.) Mill sp.	Fabaceae	*Syzygium cumini* (L.) Skeels	Myrtaceae	
		Kuhnia rosmarnifolia Vent.	Asteraceae			
		Lantana camara L.	Verbenaceae			
S. album	China	*Gardenia jasminoides* Ellis	Rubiaceae	NR		Ma et al. (2005)
		Hibiscus rosa-sinensis L.	Malvaceae			
		Phyllanthus reticulatus Poir.	Euphorbiaceae			
S. album	China	*Acacia confusa* Merr.	Fabaceae	*Bischofia polycarpa* (H. Lévl.) Airy Shaw	Euphorbiaceae	Lu (2011); Lu et al. (2013, 2014)
		Dalbergia odorifera T. Chen	Fabaceae	*Dracontomelon duperreranum* Pierre	Anacardiaceae	
S. album	China	*Kuhnia rosmarnifolia* Vent.	Asteraceae	NR		Zhang et al. (2012a)
		Acacia confusa Merr.	Fabaceae	*Bauhinia blakeana* Dunn	Leguminosae	Chen et al. (2014)
		Calliandra haematocephala Hassk.	Mimosaceae	*Delonix regia* (Hook.) Raf.	Leguminosae	
		Caesalpinia sappan L.	Fabaceae	*Leucaena leucocephala* Lam.	Mimosaceae	
		Erythrina corallodendron L.	Papilionaceae	*Ormosia pinnata* (Lour.) Merr.	Papilionaceae	

Table 2 continued

Species	Country of test	Suitable hosts	Family	Unsuitable hosts	Family	References
S. album	India	*Casuarina equisetifolia* L.	Casuarinaceae	NR		Rocha et al. (2014, 2015)
S. album	China	*Dalbergia sissoo* Roxb.	Fabaceae	*Aquilaria sinensis* (Lour.) Gilg.	Thymelaeaceae	Ouyang et al. (2015)
		Lonicera japonica Thunb.	Caprifoliaceae			

NR not reported in the study

effective as pot hosts. Annapurna et al. (2006) indicated that *Mimosa pudica* L. was the most effective host among seven hosts tested, claiming that *C. cajan* has three disadvantages: (1) rapid growth thus competing with sandalwood for light and nutrients; (2) susceptibility to fungi and insect pests; and (3) need for intensive management (frequent pruning). In contrast, *Acacia acuminata* was an effective host for *S. spicatum* (Brand et al. 1998, 2000, 2003; Brand 2009; Table 1).

In South China, sandalwood plants of different ages of development (seedlings to adult plants) need different hosts. In the seedling (pot) stage, a good host plant *Kuhnia rosmarinifolia* Vent. (Asteraceae) is usually used as the seedling host (Zhang et al. 2012a; Chen et al. 2014; Yang et al. 2014). This species is a good host plant since it is propagated by cuttings, it roots easily, and no seeds are produced, thus avoiding its dispersal. Even after seedlings are transferred to the field, *K. rosmarinifolia* serves as a good host for 1–2 years until the parasitized host dies. At this stage, some shrubs (*Tephrosia candida* Roxb. DC, *Calliandra haematocephala*, *Cajanus cajan* Millsp) and small trees (*Caesalpinia sappan* Linn, *Cerasus yedoensis* Matsum.) need to be cultivated near sandalwood trees. Among possible hosts, species of the Fabaceae are commonly used possibly since they have nitrogen-fixing *Rhizobium* species in their nodules which improve the soil environment (Li 2003; Chen et al. 2014). However, some legume species are poor hosts such as *Delonix regia* (Boj. ex Hook.) Raf., *Bauhinia blakeana* Dunn and *Cassia surattensis* F.Muell. (Chen et al. 2014). Most genera of the Rutaceae are good hosts, including *Citrus*, *Clausena*, and *Murraya.*

Lu et al. (2013) found that nodulation of the host was an important factor determining the transfer of nitrogen from the host to *S. album*, increasing the amount of N transferred by about 6-fold compared to control (non-nodulated) treatments. Seedlings were planted 10 cm apart from the host (*Dalbergia odorifera* T. Chen) in a substrate of vermiculite and perlite (2:1, v/v, pH 6.8). Nodulation of the host was enhanced by *Bradyrhizobium elkanii* DG, which was originally isolated from the active nodules of *Pterocarpus macrocarpus* Kurz. This provides a simple, but important and often overlooked, management strategy for the field production of *S. album*. Biomass production of shoots, roots, and haustoria of *S. album* were greater when grown with N_2-fixing hosts than non-N_2-fixing hosts (Lu et al. 2014; Table 1). The rhizospheric pH value of the host affects the growth of *S. album*. Optimal pH in the rhizospheric soil of almost all fine hosts ranged from 5.0 to 6.0 (Mei et al. 2011). Generally, the advantage of N_2-fixing species over non-N_2-fixing species is evidenced by the literature (Table 2). The number and size of haustoria, height, and base diameter of *S. album* showed significant

differences among different N_2-fixing hosts (Chen et al. 2014).

A recent comparative study showed that a suitable host among leguminous and non-leguminous trees could promote the growth of *S. album*. Ouyang et al. (2015) found that net photosynthetic rate, stomatal conductance, transpiration rate, and plant height in *S. album* in China were similar in two suitable hosts, *D. sissoo*, a leguminous tree, and *Lonicera japonica*, a non-leguminous vine. It was suggested that black-stained material (BSM) in the interaction of haustoria penetrating into hosts might play an important role in establishing the sandalwood host connection. In the good hosts, *L. japonica* and *D. sissoo*, the connection between the finger parenchymal cells of the haustoria and the host root cell was tight and was related to the presence of a prominent BSM while BSM in the poor host *Aquilaria sinensis* was thin. The origin of BSM and its functions remain unclear. Thus, the metabolism underlying the host preference of sandalwood needs further investigation.

The dry matter gains of *S. album* grown at 33 weeks were significantly improved when *S. album* was separately partnered with the three legume hosts, *Sesbania formosa*, *Acacia trachycarpa*, and *A. ampliceps* compared with the hemi-parasite grown with *Eucalyptus camaldulensis* or without a host (Radomiljac et al. 1999b). They proposed *S. formosa* to be best host, followed by *A. ampliceps*, *A. trachycarpa*, and *E. camaldulensis* (Radomiljac et al. 1999b). Based on assays of leaf, stem, bark, and root tissue of *S. album* and its hosts, net increases in mineral contents of *S. album* over the first 9 weeks were obtained when attached to a beneficial host. In particular, some elements such as Ca, K, P, and Na were greatest when associated with hosts richest in corresponding elements. *S. album* foliage became more abundant in Na and in some cases also in P and N compared with associated hosts. By contrast, net losses or only small gains of P, K, Ca over the study interval in *S. album* grown alone or associated with *E. camaldulensis* indicated poor nutrient uptake ability through its own root system. A previous study on mineral nutrition of *S. spicatum* with its preferred host, *Acacia acuminata*, showed high levels of K and Na, a high K/Ca ratio, and low levels of Zn in the parasite compared to the host plant (Struthers et al. 1986). In this interaction, host seedlings are planted in the first year while untreated seeds of *S. spicatum* are sown directly in the second or third year, although Woodall and Robinson (2002) found that simultaneous sowing of both *S. spicatum* and *A. acuminata* improved germination, survival, and growth of the former. Woodall and Robinson (2003) noted that *S. spicatum* parasitized 68 hosts in remnant populations in Western Australia (Table 2). These studies provide some evidence that a beneficial host can supply nutrients as a direct result of the hemi-parasitism by haustoria that form between *Santalum* species and the host root. Sahai and Shivanna (1984) observed that the addition of 30 μg/ml xenognosin, the active fraction of tragacanth gum (an exudate of a legume, *Astragalus* sp.), could effectively induce haustoria in 3-month-old *S. album* seedlings in the absence of the host.

Tennakoon et al. (1997a) found that *S. acuminatum* derived nitrogen primarily from woody N_2 fixers (legumes and *Allocasuarina*), although each host transported a characteristic set of organic nitrogenous solutes, but little or no nitrate. They concluded that only a limited direct flow of amino compounds took place between xylem streams of hosts and *S. acuminatum* (Tennakoon et al. 1997b). There were close resemblances between *S. album* and legume hosts (*S. formosa*, *A. trachycarpa*, *A. ampliceps*) in concentration and composition of xylem sap amino acids, and in the amino acid spectra of the corresponding parasite endophytic tissue, and low N levels in xylem sap of *E. camaldulensis* and dissimilarities between its amino acid composition and that of partnered *S. album* (Radomiljac et al. 1998b). The analyses of net C and N gains of *S. album* and the C: N ratios of xylem solutes of *S. album* between the parasite-host associations showed that the heterotrophic gains of C from xylem of the three legume hosts was highest in *S. album* partnered with *A. ampliceps* (57.9 % of total carbon) and lowest in *S. album* and *S. formosa* (34.6 %) over a 9-week period (Radomiljac et al. 1999b). This is similar to the study of Tennakoon et al. (1997b) in which *S. acuminatum* probably would gain more than one-third of its C requirement for dry matter production heterotrophically from the xylem of its hosts. Foliar N concentrations of *S. album* were significantly greater than corresponding hosts and higher when on the N_2-fixing hosts than on *E. camaldulensis*, or without a host (Radomiljac et al. 1999c). When *S. austrocaledonicum*, distributed in New Caledonia, was associated with *A. spirorbis*, *psydrax odorata*, *Diospyros pustulata*, or *Cleistanthus stipitatus*, an analysis of foliar mineral composition showed that nitrogen levels were particularly high when *A. spirorbis* served as the host (Veillon and Jaffré 1995). These results indicate that *Santalum* directly gained xylem N and C from N_2-fixing legumes hosts and that the parasite obtained little N and C from the xylem sap of non-beneficial hosts such as *E. camaldulensis*.

In addition, xylem sap of hosts contained variable amounts of sucrose, glucose, and fructose, whereas that of matching parasites was dominated by fructose in *S. album* (Radomiljac et al. 1998b). Similarly, the levels of sucrose, fructose, glucose, malate, and citrate were high in all saps, and fructose was especially prominent in *S. acuminatum* (Tennakoon et al. 1997b). Using ^{14}C, glucose was found to move from the host *Myoporum parvifolium* to *S. acuminatum* (Loveys et al. 2001a). Dissimilarities were also

evident in the proportional amounts of xylem-borne organic acids and sugar and organic acid composition of leaves between hosts and *S. album* (Radomiljac et al. 1998b). Chloride, sulfate and phosphate were found in the xylem of *S. acuminatum* (Tennakoon et al. 1997b). This implied that substantial metabolic patterns of incoming xylem solutes were variable between *Santalum* species. Tennakoon et al. (1997b) found that 40–80 % of proline was from the infiltration of xylem of haustoria-bearing root segments of a major host (*A. rostellifera*) and nitrate reductase activity was induced in haustoria following host xylem feeding of nitrate in *S. acuminatum*. That study concluded that haustoria act as a major site for the synthesis and export of proline and might therefore play an important role in osmotic adjustment of the parasite and its related acquisition of water from hosts in *Santalum*. An interesting finding was the transfer of an insecticidal compound with a molecular weight of 705.4, from the host *Melia azedarach* to *S. acuminatum*, which increased the mortality of apple moths fed on the fruit of *S. acuminatum* (Loveys et al. 2001a).

In *S. album*, photosynthetic rate and water-use efficiency were generally higher than in corresponding hosts while transpiration rates were not noticeably different between parasite-host associations (Ouyang et al. 2015). However, diurnal profiles of gas exchange and leaf water potential of hosts and parasites showed closely coordinated diurnal stomatal responses of the parasite water relations to its host, thus suggesting that transpiration rates of the parasite generating leaf water potential gradients led to continuous uptake of water and nutrients from the host (Radomiljac et al. 1999c). Transpiration and photosynthetic rates of *S. acuminatum* were consistently lower than those of its principal hosts, but water-use efficiencies were very similar to that of one host, *A. rostellifera* (Tennakoon et al. 1997a). A comparative study on water relations and gas exchange characteristics of *S. acuminatum* and its hosts at three examined sites, i.e., Middleback, Aldinga and Adelaide, in central Southern Australia showed that *S. acuminatum* had a higher osmotic potential than the hosts at Middleback and Aldinga sites during summer and winter, with a stable water potential difference of 1.7 MPa between them over a measurement period of 24 h, in which mannitol, Na^+, K^+ and Cl^- dominated in the osmotic potential of the parasite (Loveys et al. 2001b). Moreover, stomatal conductance and assimilation of *S. acuminatum* were also lower those of the hosts at both sites during summer and winter measurements. However, transpiration for *S. acuminatum* was different between the two sites investigated. The instantaneous water-use efficiency [(0.13–2.2 μmol (CO_2) $mmol^{-1}$ (H_2O)] of *S. acuminatum* was higher than that of the host at Middleback, expressed as lower transpirational water loss.

Dynamics of the haustoria

Root haustoria are structures of parasitic plants that form physical connections with the roots of other plants and provide a conduit between parasite and host (Irving and Cameron 2009). These haustoria are important organs for transporting water and nutrients from host to parasite. Due to the hemi-parasitic nature of sandalwood, like other members of the Santalales, their cultivation is more complex compared with other woody trees. Many studies have focused on haustorial anatomy and development and parasite physiology to better understand the mechanisms of hemi-parasitism in sandalwood.

Morphological and anatomical characters of haustorium have been widely investigated in *Santalum* (Barber 1906, 1907; Rao 1942a; Tennakoon et al. 1997a, b; Tennakoon and Cameron 2006; Zhang et al. 2012a; Yang et al. 2014). Haustoria have an inverted conical shape and their apex is horizontally round before contacting host root. Otherwise, if haustoria can encounter a suitable host, its horizontal face will attach to the host root and closely clasp it to penetrate and establish a vascular connection with that of the host root, and finally form a mature haustorium. The general anatomy of *Santalum* haustorium was similar in these studies even when sandalwood partnered with different hosts. Research has showed that *Santalum* is a xylem-feeding parasite relying on the interfacial parenchyma of finger cells of haustoria to actively transport water and solutes from the host root (Tennakoon and Cameron 2006).

Ouyang et al. (2015) studied the differences between the suitability of hosts for *S. album*. Well-formed and frequently replaced haustoria formed in a good host *Dalbergia sissoo* that likely enhanced metabolism and nutrient transport. Ultrastructural observations showed differences in the interfacial region and internal structure between finger parenchymal cells and host root cells, vascular tissue, the reaction of host root cells, and penetration modes.

Recently, a detailed study of haustorial development showed obvious morphogenic differences between haustorium formation and lateral root initiation: while the former develops laterally from the root cortex of *S. album*, in the latter, the lateral root originates from the pericycle of the mother root (Zhang et al. unpublished data). A large number of starch and proteinaceous compounds are present throughout haustorial development, especially in the stage in which haustoria invade the host root. Many lysosomes can be observed and large-scale digestion of host cells occurs at the interface between the parasite and the host (Zhang et al. 2012a). These results suggest that the haustorium is an active metabolic organ in sandalwood and that mechanical force and enzymatic activity may be needed for the haustoria to be able to penetrate the host tissues. Yang

Table 3 Explant source, size, and surface sterilization procedures for preparation of tissue culture studies of sandalwood (chronological listing)

Species	Explant source	Explant type, size and density; culture vessel	Surface sterilization and preparation	References
S. album	Mature fruit. Age of mother plant NR	Seeds, ZEs, endosperms. Exact size of explant NR. Culture tube and dimensions NR. 15 ml media/tube. Explant density NR	Fruits → CW 10 min	Rangaswamy and Rao (1963); Rao (1965); Rao and Rangaswamy (1971)
S. album	Stem segments from 4-week-old in vitro seedlings. Age of mother plant NR	Stem segments (size NR). 5 mm long hypocotyls segments from seedlings for plant regeneration and callus culture. Culture vessels NR (tubes from photos). Explant density NR	NR	Rao and Bapat (1978); Bapat and Rao (1979); Shekhawat et al. (2008, 2010)
S. album	Shoot segments and shoot tips of >20-year-old trees	5–6 mm diameter shoots cut into 5–6 mm long explants (shoot segments). Shoot tips = 5 mm. Culture vessels NR (text tubes and Petri dishes from photos). Explant density NR	Shoot segments and shoot tips → DW → 0.1 % $HgCl_2$ 10 min → SDW (multiple washes)	Lakshmi Sita et al. (1979, 1980b); Lakshmi Sita and Sobha Rani (1983); Lakshmi Sita (1986)
S. album	Green seeds (6-8 mm). Age of mother plant NR	Endosperm from seeds. Other conditions, as for Lakshmi Sita et al. 1979	NR	Lakshmi Sita et al. (1980a); Lakshmi Sita (1986)
S. album	NR	Achlorophyllous shoots derived from callus	NR	Bhaskar and Rao (1983)
S. album	Juvenile shoots from mature tree, green fruits, mature seeds	The cut ends of shoot segments were sealed with molten wax, Explant size, explant density, culture vessel type and dimensions NR (test tubes and Petri dishes assumed from photos)	Shoot segments, green fruit and mature seeds → detergent soap (conc. and duration NR) → tap water (duration NR) → 0.1 % $HgCl_2$ (w/v) 5-8 min → SDW (multiple washes)	Rao and Raghava Ram (1983)
S. album	Seeds → in vitro seedlings. Age of mother plant NR	5 mm hypocotyl segments from 4-week-old in vitro seedlings (shoot bud initiation). Hypocotyl segments with excised regenerated shoot buds (for SE). Culture vessel NR (tubes from photos). Explant density NR	$HgCl_2$ (conc. NR) 5 min → SDW (6X) → sown on BM	Bapat and Rao (1984)
S. album	Juvenile shoots from 30-year-old trees. Cut ends immediately sealed by molten wax.	1 cm long nodal segments; 1.5 cm long internode segments. Culture vessel and explant density NR	Shoots → detergent water → RTW → 0.1 % $HgCl_2$ 8 min → 6X SW	Rao et al. (1984)
S. album	4-week-old in vitro seedling. Juvenile shoots from 30-year-old tree; first 3–4 young leaves from apex. Age of mother plant NR	Protoplasts from 5 mm long hypocotyls segments of seedlings, callus culture of stem and leaves. Culture vessel NR (tubes and Petri dishes from photos). Explant density NR	Protocol for seedling and stems NR. Leaves: 0.1 % $HgCl_2$ → SDW (multiple washes)	Bapat et al. (1985)
S. album	Shoot segments of 20-year-old trees	Shoot segments → callus → suspension culture → protoplast isolation → protoplast culture → SEs. Explant size, culture vessel and explant density NR	NR	Ozias-Akins et al. (1985)
S. album	Shoot segments of 20-year-old trees. Embryogenic cell suspension cultures from 3-year-old callus cultures	Protoplast from 4 to 5-days-old suspension culture. Subculture in 100 ml Erlenmeyer flask containing 6–8 ml suspension/14 ml medium (cell suspension culture). 2 ml/6 cm Petri dish. 1–5 × 10^5 protoplasts/ml (protoplast culture)	NR	Rao and Ozias-Akins (1985)

Table 3 continued

Species	Explant source	Explant type, size and density; culture vessel	Surface sterilization and preparation	References
S. album	Young shoots from 20-year-old mother plant immediately sealed at both cut ends	Internode segments (5 mm long). Density and culture vessel NR. SEs embedded and suspended at 10 beads/flask (100 ml)	$HgCl_2$ (conc. NR) 7–8 min → SDW (multiple washes)	Bapat and Rao (1988)
S. album	Stem internodes of young shoots from 20-year-old tree	Details not available from original protocol (Bapat and Rao 1989)	Details not available from original protocol (Bapat and Rao 1989)	Bapat and Rao (1992a); Bapat et al. (1996)
S. album	4-week-old fruits. Age of mother plant NR	Endosperm. Exact size of explants, explant density and culture vessels NR	NR	Sankara Rao et al. (1996); Shiri and Rao (1998)
S. album	Tender and thicker stem shoots. Age of mother plant NR	Shoot tips, nodal explants, and leaves. Test tube (borosilicate glass, 150 mm × 25 mm or 100 mm × 25 mm). Explant density NR	RTW + few drops detergent → 1-2 DW wash (for all explants) → 0.05 % $HgCl_2$ 5 min for tender stem; 0.1 % $HgCl_2$ 5 min for thicker stem and leaves; 0.5–1.0 % $HgCl_2$ 5–10 min for shoot tip and nodal explants. Rinses NR	Muralidharan (1997)
S. album	Seeds. Age of mother plant NR	Zygotic embryo from 10 days in vitro germinated seeds	NR	Rai and McComb (1997)
S. album 'Elite Kerala'	Nodes and hypocotyls from in vitro-germinated seedlings. Age of mother plant NR	Explant size, density NR. Culture vessel NR	NR	Das et al. (1998)
S. album 614, *S. spicatum* S107	Seeds and nodes from mature, superior tree. Seeds harvested from fruit with a green to reddish pericarp	To compare with field-derived explants, in vitro-derived leaves and nodal segments were also used. Exact size of explants and age of mother plants NR. Explant density and culture vessels NR	Seeds without pericarp + single nodal segments: commercial soap (1 %) 5–10 min → 1 % NaOCl 15 min → 5X SDW	Rugkhla and Jones (1998)
S. album	Stem of 30-year-old tree. Age of seedlings NR	Stem and hypocotyl segments: size NR	NR	Bapat and Rao (1999)
S. album	Seeds → in vitro seedlings. Age of mother plant NR	Seedling hypocotyls (10–15 mm long). Density and culture vessel NR for embryogenic callus production. Embryogenic callus used for bioreactor (liquid media) and test tube (solid media) trials	NR	Das et al. (1999)
S. album	Seeds → in vitro seedlings. Age of mother plant NR	Seedling hypocotyls (size NR). Density and culture vessel NR for embryogenic callus production. Embryogenic callus used for liquid media trials in 250-ml Erlenmeyer flasks	NR	Das et al. (2001)
S. album	Endosperm. Age of mother plant NR	Endosperm callus. Culture vessel and explant density NR	NR	Anil and Rao (2000)
S. album	Endosperm from 4-week-old fruit	Endosperm → callus → callus proliferation and SE induction → PEM → SE maturation. Culture vessel and explant density NR in suspension culture. Torpedo and cotyledonary stage SE at 21 days used	NR	Anil et al. (2000)

Table 3 continued

Species	Explant source	Explant type, size and density; culture vessel	Surface sterilization and preparation	References
S. album	20-year-old candidate plus tree	Nodal segments (1.5–2.0 cm, trimmed to 1–1.5 cm after disinfection)	RTW 30 min → soap → 4 % NaOCl 4 min → 0.1 % $HgCl_2$ 10 min → SDW 2–3 min	Radhakrishnan et al. (2001)
S. album	Seeds → in vitro seedlings. Age of mother plant NR	Hypocotyls and stem nodes (size NR). Culture vessel NR	NR	Ilah et al. (2002)
S. album	Mature seeds from 50 to 60-year-old elite tree	Zygotic embryos. 200-ml glass jars with 35 ml medium/jar for induction of somatic embryogenesis. 25 × 100 mm test tubes with 15 ml medium/test tube for somatic embryo conversion to plantlets	Seeds: deionized water overnight → 2 % NaOCl + 0.005 % Tween-20 10-15 min → 3X SDW. Seeds air-dried in laminar flow bench for 10 min prior to excision of zygotic embryos	Rai and McComb (2002)
S. album	Seeds. Age of mother plant NR	GA_3 treated seeds. Culture vessel and density NR	Seeds → 0.15 % $HgCl_2$for 8 min → SDW	Sanjaya and Rai (2003)
S. album	Leaves from 3 to 4-week-old in vitro seedlings	Intact leaves or half leaves (sections cut perpendicular to the mid-vein) 5–15 mm long; adaxial and abaxial surfaces of the laminae tested separately	Seeds: 0.1 % $HgCl_2$ 4 min → 3X SDW	Mujib (2005)
S. album	In vitro shoots derived from in vitro subcultured shoots. Age of mother plant NR	Shoot tip size and age of donor plant NR. Jam bottles (13 cm high, 7 cm diameter)	NR	Primawati (2006)
S. album	Nursery seeds (for rootstocks; 2006a) and 50–60-year-old tree (high-yielding oil: 4–5 %; 2006a, 2006b) for scions	Nodal shoot segments (2.5–3.5 cm long) with dormant axillary buds, harvested in Nov-Jan. 25 × 100 mm test tubes (one seed/tube; 25 ml medium/tube)	Decoated seeds for in vitro rootstocks (2006a): 0.05 % GA_3 overnight → 0.075 % $HgCl_2$ 6-7 min → 6-8X SDW. Nodal segments from 50-60-y-old tree for scions (2006a, 2006b): 70 % EtOH 30-40 s → 0.075 % $HgCl_2$ 6–7 min → 6-8X SDW	Sanjaya et al. (2006a, b)
S. album	Mature stem segments from elite tree (age NR)	1 cm long stem segments (nodes or internodes?). 100 ml Erlenmeyer flasks: 200 mg of friable embryogenic callus tissue in 20 ml of liquid medium	0.1 % $HgCl_2$ 5 min → 2-3X SDW	Shekhawat et al. (2008)
S. album	Young shoots from elite mature tree (age NR)	1 cm long stem segments, 80 × 150-mm (diameter × height) culture jars, explant density NR	Young shoots → RTW 30 min → 0.1 % $HgCl_2$ 10 min → SDW 3X	Ma et al. (2008)
S. album	Top shoots, young leaves, and seeds. Age of mother plant NR	Top shoots, leaves of 0.5 cm^2, seeds	Top shoots and leaves → 0.1 % $HgCl_2$ 10 min → SDW 5X Seeds → RTW → peel pericarps → 0.1 % $HgCl_2$ 10 min → SDW 5-6X	Mo et al. (2008)
S. album	Fruits collected in May from tree (age NR)	Seed. Viability tested with 2,4,5-triphenyl tetrazolium chloride (TTC) before use. 1 or 2 seeds/culture tube	Fruits soaked overnight in water → DW 3X → soap solution 30 min → 0.1 % $HgCl_2$ 3 min → SDW 3X. Seeds → 0.1 % $HgCl_2$ 3 min → SDW 3X → 4 mM GA_3 12 h → SDW 3X	Nikam and Barmukh (2009)

Table 3 continued

Species	Explant source	Explant type, size and density; culture vessel	Surface sterilization and preparation	References
S. album	Immature seeds and mature seeds, 10-year-old tree	ZEs	Seeds → peel pericarps → 70 % EtOH 1 min → 5-10 % NaClO 5–20 min → 0.1 % $HgCl_2$ 5-15 min → SDW 4-5X	Mo et al. (2010)
S. album	Seeds of 8-year-old plants → in vitro seedlings	Internodes (8–10 mm) from 2-months-old seedlings. 25 × 150 mm culture tubes. Explant density NR	Seeds: RTW 20 min → ~ 2 % Tween-20 1 min → SDW → 0.1 % $HgCl_2$ 5 min → 4X SDW. Pericarp removed	Janarthanam and Sumathi (2011); Janarthanam et al. (2012)
S. album	Potted greenhouse plants (age NR)	Nodes, internodes, juvenile leaves and shoot tips	Seeds: Samantray and Upadhyaya (2010) protocol. 4 explants: RTW → 70 % EtOH → 0.1 % $HgCl_2$ 5 min → 3-5X SDW	Revathy and Arumugam (2011)
S. album, *S. yasi*, R1 hybrids	10–15 cm side branches of 10–12 year-old trees collected in Jan and May–June	Juvenile nodal segments (5–7 cm long) → cut into 1 cm nodal segments 0.5 cm above and 0.5 cm below the nodes → leaf nodes. Culture in McCartey bottles or polycarbonate tubes. Explant density NR	Leaf nodes → tap H_2O + bleach (4.2 % NaClO) time NR → tap H_2O → SDW → 70 % EtOH 1 min → 100 mg/l citric acid → 4.2 % NaClO + 2–3 drops Tween time NR → SDW a few times	Baiculacula (2012)
S. album	Leaves from 3 to 4-week-old in vitro and ex vitro seedlings	Leaf disks (squares of 5–8 mm). Petri dishes	Seeds: 0.1 % $HgCl_2$ 4 min → 3X SDW. *Ex vitro* leaves (1^{st} and 2^{nd} from apex): collected in DW → RTW 30 min → DDW + 2 % Tween-20 20 min → 1 % Bavistin 10 min on shaker at 30 rpm → 70 % EtOH 1 min → 0.2 % $HgCl_2$ 10 min (in 100 psi vacuum) → 4-5X SDW	Bele et al. (2012)
S. album	Hypocotyl segments from 5-week-old seedlings	Hypocotyls and crown section (3–10 mm long), cotyledon and leaf pieces (10–16 mm^2 surface area), root segments (3–5 mm long) from 5 and 10 DAG. Test tubes and Petri dishes	Seeds: 2.5 % NaOCl 2 h → 3 washes in SW (20, 10, 5 min each) → testa removed for in vitro SG	Crovadore et al. (2012)
S. album	Leaves from mature trees (age NR)	10 cm^2 trimmed to 4 cm^2. Final sterilized explant = 10-15 mm. One explant per test tube (150 × 25 mm)	0.1 % Tween-20 5 min → 4–5 washes in DW → 1 g/l Bavistin, 0.2 g/l cefotaxime, and 0.2 g/l kanamycin 10 min → 3X SDW → 0.1 % $HgCl_2$ 3–4 min → 6-8X SDW	Singh et al. (2013)
S. album	Nodes from young branches (age NR)	2-3 cm nodes	According to Singh et al. (2013)	Singh et al. (2015)

Table 3 continued

Species	Explant source	Explant type, size and density; culture vessel	Surface sterilization and preparation	References
S. album	Nodes from 2-year-old plant potted along with *Desmodium* and *Alternanthera* sp. Mother plants was treated with fungicide (Tilt 10 ml/l) once in a week and Topsin 5 g/l and Thiram 1.4 g/l spreyed alternatively to mother plant. Albert solution 50 ml/l applied weekly (composition of Albert solution or Reference is NR). Explants collected in morning	2 cm nodes and mature and immature seeds (green pericarp still attached to mother plant)	Soap water 5 min → RTW 30 min → 2 g/l Captan ™ 30 min → 15 % Clorox™ 15 min → 70 % EtOH 10 min → 3X SDW	Peeris and Senarath (2015)

BM basal medium (in mg/l: $KINO_3$ (1900), NH_4NO_3 (1650) $CaC1_2.2H_2O$ (440), $MgSO_4{\cdot}7H_2O$ (370), KH_2PO_4 (170), $MnSO_4{\cdot}4H_2O$ (25), H_3BO_3 (10), $ZnSO_4{\cdot}7H_2O$ (13.9), Na_2EDTA (18.6), *myo*-inositol (100), nicotinic acid (5), folic acid (5), glycine (2), pyridoxine–HCl (0.5), thiamine-HCl (0.5), biotin (0.05), sucrose (20 g/l), Difco bacto agar (6 g/l) modified WB according to Rangaswamy (1961)), *CW* chlorine water, *DAG* day(s) after germination, *DW* distilled water, *DDW* double distilled water, *EtOH* ethyl alcohol (ethanol), GA_3 gibberellic acid, $HgCl_2$ mercury chloride, *NaOCl* sodium hypochlorite, *NR* not reported in the study, *PEM* pro-embryogenic masses, *rpm* revolutions per minute, *RTW* running tap water, *SDW* sterilized (by autoclaving) distilled water, *SW* sterile water, *ZE* zygotic embryo

et al. (2014) found that the inter-collapsed layers, an important structure within haustoria, might be involved in cell inclusion and energy concentration at the inner meristematic region and these cell inclusions and energy were recycled to affect penetration, to reinforce the physical connection between the haustorium and host root, and to supply space for haustorial development in *S. album*.

Haustoria can form within 30 days after germination without the need for induction by haustoria-inducing factors (HIFs) (Barrett and Fox 1997). The molecular mechanisms involved in haustorial development of *S. album* were explored based on global transcriptome analysis by *de novo* assembly (Zhang et al. 2015). A substantial number of differentially expressed genes (DEGs) were involved in cell wall metabolism and protein metabolism, as well as mitochondrial electron transport functions during haustorial development. This is in agreement with anatomical observations of haustoria development in which prolific protein synthesis actively occurred and cell walls in the host root tissue were degraded and cell membranes disintegrated in the interface of haustoria and the host root (Zhang et al. 2012a). Radomiljac et al. (1999b) noticed that the number of haustoria formed by *Santalum* on roots of different hosts was poorly correlated with host quality. A previous study indicated that endogenous levels of IAA, CK, GA_3, and ABA were higher in haustoria than in seedling roots, suggesting that phytohormones play an important role in haustorial development (Zhang et al. 2012a, 2015). The authors found that auxin signal transduction might be essential for haustorial initiation and that GAs play an important role throughout haustorial developmental processes (Zhang et al. 2015). This result also provides vital clues for artificially increasing the number of haustoria to improve growth by exogenous application of plant growth regulators in an in vitro environment. Genes encoding nodulin-like proteins might be important candidate genes for haustorial morphogenesis in *S. album* based on nodulation genes (ENODs) and related proteins found in legume nodule formation (Legocki and Verma 1979; Kalo et al. 2005; Smit et al. 2005; Zhang et al. 2015). The elucidation of this interesting question in the future probably could explain one cause for haustorial formation without of the presence of HIFs in the root hemi-parasite, S. *album* (Zhang et al. 2015).

Applied biotechnologies

In vitro culture, tissue culture, and micropropagation

This section provides an overview of the principal trends and key observations of the literature as described in

Table 4 In vitro conditions for tissue culture studies of sandalwood (chronological listing)

Studied sandalwood[a]	Culture medium, PGRs, additives, subcultures[b]	Culture conditions[c]	Experimental outcome, maximum productivity, acclimatization and variation	References
S. album	mWM + 20 % CM + 400 mg/l CH (SGM). mWM + 2 mg/l 2,4-D + 5 mg/l Kin + 0.25 % YE (seed culture). pH 5.8. 4 % sucrose. Difco bacto agar 0.8 %	PP NR. Diffused light (LI NR). 25 ± 2 °C. 50–60 % RH	SG produced seedlings in 5 weeks. In seed culture, 30–40 % of seeds initially started to germinate but did not convert to seedlings. 60–70 % of cultures showed no sign of germination. Callus formed from endosperm after 3–4 weeks: subculture produced friable callus in 4–6 weeks. Excised ZEs unresponsive	Rangaswamy and Rao (1963); Rao (1965)
S. album	mWM + CH or CM or CH + CM (SGM and subculture for cotyledon-derived callus). mBM + 2,4-D or Kin or YE alone, or in combination (ZE and endosperm culture). mBM + CH + CM (excised ZE). CH 400 mg/l; CM 20 %; YE 0.25 %. pH 5.8. Carbon source NR. 0.8 % Difco bacto agar	PP NR. Diffuse light (400–600 lux). 25 ± 2 °C. RH NR	SG on BM + CH or CM or both. ZEs and endosperm did not respond. Plantlets obtained from embryoids formed from ZE-derived callus. Germinated seedlings did not develop haustoria. Undifferentiated callus from cotyledons produced embryoids then plantlets. Excised ZE cultured for 3–4 weeks formed normal seedlings then plantlets after 2 weeks	Rao and Rangaswamy (1971)
S. album	BM or BM + 1 mg/l [IAA, IBA, NAA, NOA, Kin, BA, Zea, SD 8339, or AdS], 0-2 mg/l (NAA + Kin) or 0–2 mg/l (NAA + BA) (SIM). BM + 1 mg/l 2,4-D or pCPA or 1 mg/l (2,4-D + Kin) or 1 mg/l (2,4-D + BA) (CIM). BM + 0.5 mg/l NAA + 0.5–5 mg/l IBA (RIM)	PP NR. Fluorescent light. 1000 lux. 25 ± 2 °C. RH 55–60 %	Only hypocotyl explants responded well on BM fortified with cytokinins. Shoot segments did not respond. Callus prolific on 2,4-D + BA media. 2 mg/l BA produced 15–20 buds/explant. Complete plantlets regenerated in 4–8 weeks. Rooting obtained only in few cultures (data NR). Acclimatization NP	Rao and Bapat (1978)
S. album	Liquid BM (same as Rao and Bapat 1978) + NAA or IAA (1 mg/l), 2,4-D (1 mg/l), BA (1 mg/l), GA**** (1 mg/l), CM (10 %), NAA (1 mg/l + BA (1 mg/1), or CM (10 %) + CH (400 mg/1) (SEMM) (liquid culture in gyrator shaker at 120 rpm continuously for 4 w). Solidified BM + BA (1-12 mg/l), 2,4-D (1 mg/l), 2,4-D (1 mg/l) + CM (10 %), 2,4-D (1 mg/l) + CH (400 mg/1), or 2,4-D (1 mg/l) + YE (400 mg/l) (SEIM). BM + IAA (1 mg/1), NAA (1 mg//1) or BA (1 mg/1) (SEMM)	PP NR. Fluorescent light. 1000 lux. 25 ± 2 °C. RH 55–60 %	After 4 weeks of callus subculture, globular SEs converted to plantlets and planted in soil (30 % on BM + 1 mg/l IAA). Plantlets acclimatized in soil after 8 weeks (watered with Hoagland's solution; other acclimatization conditions NR)	Bapat and Rao (1979)
S. album	MS + 1 mg/l 2,4-D + 0.2–0.5 mg/l Kin (CIM). MS + 1 mg/l GA_3 (SEIM). MS or MS + 1 mg/l GA_3 + 1-2 mg/l IAA + 0.1 mg/l 2,4-D or MS + 0.5 mg/l BA + 1 mg/l NAA (SEMM). WB or WB + 0.5 mg/l IAA (RIM). pH 6.0. 2 % sucrose. Gelling agent NR	12-h PP. CWFT. 400 lux. 26 ± 1 °C	Callus formed from shoot tips and shoot segments. Embryoids formed within 4–5 weeks from callus. Organogenesis not quantified. Acclimatization NP. Callus used to isolate protoplasts in 1983 study	Lakshmi Sita et al. (1979)[e]; Laxmi Sita and Sobha Rani (1983); Lakshmi Sita (1986)

Table 4 continued

Studied sandalwood[a]	Culture medium, PGRs, additives, subcultures[b]	Culture conditions[c]	Experimental outcome, maximum productivity, acclimatization and variation	References
S. album	MS + 1-2 mg/l 2,4-D or MS + 0.5–2 mg/l BA + 1 mg/l NAA (CIM). MS + 1 mg/l 2,4-D (callus subculture). MS + 1–2 mg/l GA_3 (SEIM). MS + 0.3 mg/l BA + 1 mg/l IAA + 0.3 mg/l Kin + 1 mg/l GA_3 (SEMM). WB + 0.5 mg/l IAA (RIM). Shake cultures using callus in 250-ml flasks at 70 rpm and pH 5.2 (1980b). Other conditions as for Lakshmi Sita et al. (1979), or unclear	As for Lakshmi Sita et al. 1979	Embryoid formation in 4–6 weeks. Organogenesis not quantified. Acclimatization NP	Lakshmi Sita et al. (1980a)[e], b; Lakshmi Sita (1986)
S. album	1–3 mg/l NAA (RIM). Other conditions NR	NR	*In vitro*-derived shoots cultured in pots with host *Cassia siamea*, leading to plantlet formation	Bhaskar and Rao (1983)
S. album	MS + 1 mg/l 2,4-D alone or in combination with 0.2 mg/l Kin (CIM). MS + 1 mg/l IAA + 1 mg/l BA (SEIM). MS + 1 mg/l IAA + 0.5 mg/l IBA + 0.5 mg/l GA_3 (SE germination). pH, 5.8. 2 % sucrose (CIM) or 5 % (SEIM, SE germination). 0.6 % agar	Continuous light. 1000 lux. 25 ± 2 °C. 55 % RH. At SE germination stage, cultures kept in dark for 72 h then transferred to continuous light for 4–6 weeks	Within 3 weeks, callus formed on surface of endosperm. During 6 weeks, callus proliferated well. SE formation observed within 4 weeks from callus obtained on CIM. Plantlets with 2–3 pairs of leaves with roots developed within 4 weeks and transferred to vermiculite then acclimatized in earthen pots with soil	Rao and Raghava Ram (1983)
S. album	mBM + 1 mg/l NAA or 1 or 2 mg/l BA (SIM). mBM + (0.5 mg/l NAA + 5 mg/l IBA) or 1 mg/l BA (RIM). mBM + 0.5 mg/l or 1 mg/l IAA (SEIM). mBM + 0.4 % YE + 400 mg/l CH + 400 mg/l CA (SEMM). mBM + 1 mg/l IAA or NAA (PCM)	PP NR. CWFT. 1000 lux. 25 ± 2 °C. RH 55–60 %	Normal plantlets produced (time period NR). Acclimatized for 3 w in Hoagland's nutrient solution (Hoagland and Arnon 1938). 10 % survived in field without host plant. 90 % of the basal region of hypcotyl explants differentiated into buds. Insignificant effect of seedling age. Rapid response on liquid medium than on agar medium. 100 % response on hypocotyl explant orientated with root end in direct contact with medium. 20 cm long plantlets obtained on RIM. 4 % sucrose + 1650 mg/l NH_4NO_3 best for SE induction	Bapat and Rao (1984)[e]
S. album	MS + 0.5 or 1 mg/l BA (SIM). MS + 1 mg/l 2,4-D or MS + 1 mg/l 2,4-D + 0.2 mg/l Kin (CIM). MS + 1 mg/l IAA + 1 mg/l BA (SEIM). 2 % sucrose. 0.7 % agar. pH 5.6. MS + 1 mg/l IAA + 0.5 mg/l IBA + 0.5 mg/l GA_3 (SEMM). 5 % sucrose. 0.6 % agar	Initial 72 h darkness for root induction. All other conditions as in Bapat and Rao (1984)	Shoot buds obtained from nodes did not respond to rooting. Shoots obtained from SEs of internode-derived callus resulted in successful plantlet conversion and 10 % survival in field conditions	Rao et al. (1984)[e]

Table 4 continued

Studied sandalwood[a]	Culture medium, PGRs, additives, subcultures[b]	Culture conditions[c]	Experimental outcome, maximum productivity, acclimatization and variation	References
S. album	MS + 1 mg/l 2,4-D or BA (CIM for hypocotyl). MS + 1 mg/l 2.4-D or 1 mg/l 2,4-D + 0.5 mg/l Kin (CIM for stem). MS + 1 mg/l 2,4-D (PCM for hypocotyl callus). MS + 1 mg/l IAA + 1 mg/l BA (SEIM from stem callus). Modified V47 medium + 1 mg/l 2,4-D + 1 mg/l NAA + 1 mg/l BA (protoplast proliferation medium for stem callus). MS + 1 mg/l IAA or MS + 1 mg/l IAA + 1 mg/l BA, or ½ MS + 1 mg/l IAA or ½ MS + 10 % CM + 500 mg/l CH (SEIM from stem callus). SEMM NR. Medium for leaf-derived protoplast culture NR	As for Bapat and Rao (1984)	Effect of explant source on protoplast isolation efficiency. Maximum number of SEs induced on stem-derived callus cultured on ½ MS + 1 mg/l IAA. Plantlet conversion from stem callus-derived SEs. No SE induction from leaf- and hypocotyl-derived callus	Bapat et al. (1985)[e]
S. album	CIM NR → suspension culture (composition NR) → subculture (0.5 or 1 mg/l 2,4-D) → liquid or gelled media (0.1–2 mg/l BA) (details NR) → protoplast isolation → V47 medium (750 mOs/kg H_2O, adjusted using mannitol) (PCM) → MS medium (IBA + BA conc. NR). Gelling agent, pH, carbon source and other conditions NR	NR	SEs obtained from protoplast derived culture. Organogenesis not NR but complete plants claimed to have formed from SEs	Ozias-Akins et al. (1985)[e]
S. album	MS + 2,4-D (0.5–2.5 mg/l) + 1 mg/l folic acid (liquid SEIM). 3.4 % sucrose (CSC). Liquid MS or MS + agar either with Zea (0.2, 0.35 mg/l), BA (0.1, 0.5, 1.0, 2.0 mg/l) or BA (0.1, 0.5, 1.0, 2.0 mg/l) + 0.01 mg/l 2,4-D (SEM). MS or ½ MS, alone or MS or ½ MS + BA (0.1 or 1 mg/1) or 1 mg/l IAA or 1 mg/l GA_3 + 0.2 mg/l BA (SEMM). MS + agar or filter-paper bridge on mWBM + 0.5 mg/l IAA or combination of 0.1 mg/l IAA + 0.5 mg/l IBA + 0.5 mg/l GA_3 (SGM). Protoplast culture: V47 medium (750 mOs/kg H_2O). pH 5.8 (PCM). MS + 1 mg/l IAA + 1 mg/l BA or 400 mg/l casamino acid (SEIM from protoplasts). MS + 1 mg/l BA (SEMM from protoplasts). WM + 0.5 mg/l IAA (plantlet conversion from callus-derived SE). ½ MS (only major elements?) or WM + 1 mg/l IAA or 0.5 mg/l IBA or 1/3 mg/l GA_3 + 4 or 5 % sucrose + 0.6 % agar (germination for SE from protoplasts). Subculture cell suspension cultured every 4–5 days	PP NR. Continuous diffused light. LI NR. 26 °C. Gyrotary shaker at 150 rpm (for suspension culture)	Club and heart shaped stages of SE obtained from different callus cell lines on media with BA and 2,4-D. Secondary SEs obtained from cell suspension culture on MS containing 0.1 and 1 mg/l BA. SE successfully converted to plantlets. SEs from protoplast did not form roots	Rao and Ozias-Akins (1985)

Table 4 continued

Studied sandalwood[a]	Culture medium, PGRs, additives, subcultures[b]	Culture conditions[c]	Experimental outcome, maximum productivity, acclimatization and variation	References
S. album	MS + 1 mg/l 2,4-D (CIM). MS + 0.3 mg/l IAA or 0.5 mg/l GA (SEIM, as a suspension culture). MS + 0.5 mg/l BA + 0.5 mg/l IAA (secondary SEs). Gelling agent and pH NR. 5 % sucrose for SE germination	Suspension of beads under continuous light. 950 lux. 25 ± 2 °C	Embryogenic cells encapsulated in 3 % alginate bead showed plantlet conversion after 16 weeks. However, low synseed germination (10 %)	Bapat and Rao (1988)[e]
S. album	MS + 87.6 µM sucrose + 4.52 µM 2,4-D (CIM). MS + IAA 2.85 µM + BA 2.22 µM + 87.6 µM sucrose (SEM). MS + 87.6 µM sucrose or WM + 58.4 µM sucrose (SEIM) for 4 w. WM + 58.4 µM sucrose + 18.92 µM ABA (plantlet conversion) 2. Synthetic seed: Encapsulation of SE according to Bapat and Rao (1988)	Suspension of beads under continuous light. 1000 lux. 25 ± 2 °C. 80 rpm	SEs isolated and desiccated for 10, 20 or 30 days. One lot of desiccated SEs encapsulated in 3 % sodium alginate gel (control = non-encapsulated SEs). Both encapsulated and non-encapsulated SEs showed revived growth after rehydration on WM and developed into plants. The desiccation tolerance and regeneration of plants was dependent on the pre-treatment given to SEs. In Bapat et al. 1996, the addition of a cyanobacterial extract (*Plectonema boryanum* strain UTX594) promoted callus formation in the absence of PGRs	Bapat and Rao (1992a); Bapat et al. (1996)[e] (using protocol originally from Bapat and Rao (1989)
S. album	MS + 1 mg/l 2,4-D + 1 mg/l BA or 2 mg/l 2,4-D + 0.5 mg/l Kin (CIM). MS + 1 mg/l 2,4-D + 3 % sucrose (SEIM). PGR-free MS + 2 % mannitol (SE differentiation). PGR-free ½MS with or without mannitol (SE maturation). 0.6 % agar	NR	4 stages of somatic embryogenesis claimed, with distinct biochemical profiles	Sankara Rao et al. (1996)[e]
S. album	MS + 0.5 µM BA + 0.5 µM Kin (SIM). MS + 0.5-4 µM 2,4-D (CIM). MS + 0.5–2 µM IBA (RIM). pH 5.7. 2 % sucrose. 0.5 % agar. Subcultured every 4 weeks	16-h PP. CWFT. 18 µE m^{-2} s^{-1}. 25 ± 2 °C	Callus produced from intermodes on CIM. 4 shoot buds/nodal explant on SIM. Shoot tips failed to respond. Plant regeneration was not possible	Muralidharan (1997)
S. album	MS + 20 % CM + CH or 1 µg/l Kin (SGM; 1997). MS + 2 mg/l BA (1997) or 4.5 µM TDZ (2002) (SEIM). PGR-free MS (SEMM). ½MS + 0.5 mg/l IAA (1997) or 2.8 µM GA_3 (2002) (SE conversion). pH 5.8. 3 % sucrose. 0.8 % agar (SEIM, SEMM) or 0.15 % Phytagel (SE conversion)	16-h PP. Light source NR. 40 µmol m^{-2} s^{-1}. 25 ± 1 °C	91.6 % of explants induced SEs, forming 14.23 SEs/explant after 8 w. 91.6 % of primary SEs formed secondary SEs, forming 20.5 SEs/primary SE after 8 weeks. 81.2 % of SEs germinated after 8 w. From the same treatment, 72.3 % of plants survived in the field after initial acclimatization in sand + soil + FYM (2:1:1) and 1-2 seeds of red gram (*Cajanus cajan*) as the primary pot host. Most details not explained in 1997 paper	Rai and McComb 1997[e], (2002)[e]
S. album 'Elite Kerala'	MS minerals + B_5 vitamins + 0.5 mg/l BA (SIM). MS minerals + B_5 vitamins + 0.5 mg/l BA + 0.5 mg/l IAA (SEIM). pH 6.0. 4 % sucrose	PP NR. CWFLT. 1500 lux. 26 ± 2 °C. 60–70 % RH	25–60 shoots/SEs from hypocotyls, and only 3–5 from nodes	Das et al. (1998)[e]

Table 4 continued

Studied sandalwood[a]	Culture medium, PGRs, additives, subcultures[b]	Culture conditions[c]	Experimental outcome, maximum productivity, acclimatization and variation	References
S. album 614, *S. spicatum* S107	MS + 5 μM BA (SIM). MS + 5 μM BA + 2 μM GA_3 (for leaf enlargement). MS + 1-2 μM TDZ (SEIM). MS + 6 μM IAA + 1 μM Kin (SEMM). MS + 6 μM GA_3 (SE germination) → 3 μM GA_3 (SE elongation) (*S. album*) and with 250 mg/l CH + 5 % CW (*S. spicatum*). 6-w subculture in SEIM, then 3-w subculture during SE maintenance. pH 5.8. 2 % sucrose. 0.2 % gelrite	SEIM: PP and light source NR. 2 μmol m^{-2} s^{-1}. SEMM: 16-h PP. Light source NR. 50 μmol m^{-2} s^{-1}. 25 ± 1 °C	*S. album* nodal segments: 100 % explants formed green SEs, 72 % formed white SEs (2 μM TDZ), 64 % formed friable embryogenic tissue (2 μM TDZ). *S. album* seed: 0 % explants formed green SEs, 96 % formed white SEs and friable embryogenic tissue (2 μM TDZ). *S. spicatum* nodal segments: 20 % of explants formed primary and secondary SEs. Rooting was problematic but overall plantlet growth was improved on liquid medium. Acclimatization NP	Rugkhla and Jones (1998)
S. album	MS + 1 mg/l 2,4-D + 1 mg/l BA (CIM). MS + 1 mg/l 2,4-D for 3 w (SEIM). PGR-free MS + 2 % mannitol (SE differentiation). PGR-free ½MS with or without mannitol → WB + 0.5 mg/l IAA (SE → plantlets). 3 % sucrose. Agar conc. NR	14-h PP. CWFT. 5 (callus, SEs) → 200 (plantlets) μE m^{-2} s^{-1}. 26 ± 2 °C	Pricked torpedo–cotyledonary stage SEs (0.75–1.2 cm) from a Sankara Rao et al. (1996)-derived line. Plantlets ardened to the greenhouse simply by growing on paper bridges overlaying liquid WB. SEs genetically transformed with *Agrobacterium tumefaciens* harboring LBA4404/pKIWI105 (see text for details). Success of regeneration and genetic transformation not quantified	Shiri and Rao (1998)[e]
S. album	MS + 1 mg/l IAA (SEIM). No other SEIM conditions described. Initial pH (bioreactor) 5.8. 2000 ml in a 3.5-L airlift bioreactor (25 g embryogenic callus/l). MS + 1 mg/l BA + 0.5 mg/l ABA (bioreactor). Air-flow = 1 vvm. 3 % sucrose	16-h PP. CWFT. 24 μmol m^{-2} s^{-1}. 24 ± 2 °C. 60–70 % RH	3000 seedlings derived from bioreactor in 6 w (vs 800 in 12 w on solid medium): 59.3 % vs 88.9 % abnormality and 31.1 vs 7.7 SEs/10 ml in former vs latter, respectively	Das et al. (1999)[e]
S. album	MS + 1 mg/l BA + 1 mg/l 2,4-D (CIM). MS + 1 mg/l 2,4-D (SEIM). Liquid MS (PGR-free) + 2 % mannitol (SEMM). Orbital shaker at 100 rpm. 3 % sucrose. 3.9 mM $CaCl_2$. Gelling agent and pH NR	PP and light source NR. Diffused light of 5 μEm^{-2} S^{-2}. 26 °C ± 2 °C	Embryogenic callus consisted of two types of cells: (a) more cytoplasm that formed clumps; (b) less cytoplasm and elongated shape. Torpedo and bipolar stages of SE collected after 21 days of culture from first type of cells	Anil and Rao (2000)
S. album	MS + 4.52 mM 2,4-D (CIM; 2-w subcultures). MS + 2.85 mM IAA + 3.99 mM BA (SEIM 1; subcultures NR). WPM + 2.85 mM IAA + 3.99 mM BA + 40 mM glutamine + 0.33 M mannitol + 11.6 mM nitrate + 7.89 mM ammonium + 1.31 mg/l ABA (SEIM 2; subcultures NR). 50 ml medium in 250-ml Erlenmeyer flasks (12 g embryogenic callus/l; 75 rpm). 3 % sucrose (CIM, SEIM 1) or 4 % (SEIM 2). pH NR	Light conditions NR. 25 ± 2 °C	57.35 % optimization of SE production. SEs produced in 14 days	Das et al. (2001)[e]

Table 4 continued

Studied sandalwood[a]	Culture medium, PGRs, additives, subcultures[b]	Culture conditions[c]	Experimental outcome, maximum productivity, acclimatization and variation	References
S. album	MS + 4 mg/l BA (CIM, SIM). MS + 3 mg/l IBA (RIM). pH 5.7. 2 % sucrose. 0.9 % agar	16-h PP. Light source NR. 1000 lux. 25 ± 2 °C	Callus induced after 3 weeks. The inclusion of a seed extract of *Cajanus cajan* (red gram) in RIM did not improve rooting	Radhakrishnan et al. (2001)
S. album	BM NR + 2.26 μM 2,4-D or 2.68 μM pCPA (CIM). BM NR + 2.70 μM NAA + 2.22 μM BA (SEIM). WPM (PGR-free) (SEMM). 5.71 μM IAA (RIM). pH, carbon source, gelling agent NR	PP and light source NR. 24 μmol m^{-2} s^{-1}. 24 ± 2 °C. 70–80 % RH	2-w-old initial callus induced on CIM transferred to SEIM. Liquid medium superior to solid medium (depending on stage of SE). 53–68 % of cultures showed abnormalities (aggregation of pro-embryos and SEs, growth arrest, browning of SEs, SEs with no or poorly developed roots, roots with undeveloped shoot). 83 % rooting	Ilah et al. (2002)[e]
S. album	PGR-free MS (seed germination). MS + 11.12 μM BA (SIM). 3 % sucrose. 0.6 % agar	16-h PP. Light source NR. 40 μmol m^{-2} s^{-1}. 25 ± 2 °C	45-d-old seedlings used as rootstock in micrografting. The larger the scion used, the more successful the micrograft: 1-2 cm scions resulted in 60 % graft success	Sanjaya and Rai (2003)
S. album	MS + 0.44 and 2.22 μM BA (SIM). pH 5.8 (MS) or 5.2 (WPM). WPM + 5.71 μM IAA (RIM). 3 % sucrose. 0.8 % agar	16-h PP. CWFT. LI NR. 25 ± 2 °C	Direct shoot formation from leaf explants (13–20/explant) within 20–25 days. No auxins could induce shoots. Approx. 4-fold higher shoot bud production in liquid medium than in solid medium. Epiphyllous shoots produced when explants placed in horizontal position, but not when in the vertical position, but shoots from these buds developed slowly	Mujib (2005)
S. album	MS + 1.5 mg/l BA + 0.2 mg/l Kin + 100 mg/l glutamine (shoot tip development medium). 3 % sucrose	NR.	1.4 shoots/shoot tip. No rooting or acclimatization experiments. 17 % browning and contamination	Primawati (2006)
S. album	PGR-free MS (SGM for rootstocks). MS + 0.53 μM NAA + 11.09 μM BA (SIM). MS (liquid) + 2 % sucrose on paper bridges (post-grafting). Subculture every 4 w. pH 6.0. 3 % sucrose. 0.6 % agar	12-h PP. CWFT. 60 μmol m^{-2} s^{-1}. 28 ± 1 °C	Seeds were germinated in vivo and in vitro to assess micrografting, and 45-days-old seedlings served as rootstocks. In vitro shoots (0.5–2.0 cm long) derived from third subculture were used as scions. 60 % of grafts were successful. 8-week-old grafted plantlets were successfully acclimatized (% success NR) in sterilized soilrite (60 μmol m^{-2} s^{-1}; 25 ± 1 °C)	Sanjaya et al. (2006a)
S. album	MS + 0.53 μM NAA + 11.09 μM BA (SIM). SIM + 283.93 μM AA + 118.1 μM CA + 104.04 μM cysteine + 342.24 μM glutamine + 10 % CM (SMM). ¼MS + 2 % sucrose after 48-h pulse in 98.4 μM IBA. Subculture every 4 w. pH 6.0. 3 % sucrose. 0.6 % agar	12-h PP. CWFT. 60 μmol m^{-2} s^{-1}. 28 ± 1 °C. 60–65 % RH	4.92 shoots/sterilized nodal shoot segment in initial culture and 4.63 shoots/in vitro nodal shoot segment during shoot multiplication. 41.7 % of shoots could root in vitro. 50 % of shoots could root in soilrite after treatment with 1230 μM IBA. 100 % survival of field-grown plantlets	Sanjaya et al. (2006b)

Table 4 continued

Studied sandalwood[a]	Culture medium, PGRs, additives, subcultures[b]	Culture conditions[c]	Experimental outcome, maximum productivity, acclimatization and variation	References
S. album	MS + 5.0 µM BA + 0.5 µM NAA (adventitious shoot propagation) + monthly subculture. MS + 250 µM IBA (RIM). pH 5.6. 3 % sucrose. 0.6 % agar	14-h PP. CWFT. 40 µmol m^{-2} s^{-1}. 25 ± 2 °C	5.7 shoots/shoot explant after 1 month of culture. Some adventitious roots within 1–3 months. 8 % of shoots formed roots. 95 % survival of acclimatized plantlets in sand: peat soil: organic matter (1:1:1) after 2 months of acclimatization in greenhouse and watered each day. Greenhouse growth conditions NR	Ma et al. (2008)
S. album	MS + 1 mg/l BA, MS + 1 mg/l 2,4-D, or MS + 0.5 mg/l TDZ (CIM). Subcultured twice for globular SE induction. MS + TDZ, MS + GA_3, or ½ MS + GA_3 (SE germination). pH NR. 4 % sucrose. Gelling agent NR	16-h PP. CWFT. 1500 lux. 25 ± 1 °C	On MS + TDZ for SE induction: 91.2 % induction. SE germination = 100 % on MS + GA_3 + 4 % sucrose, but no roots formed	Mo et al. (2008)
S. album	MS + 1 mg/l 2,4-D + 0.2 % Phytagel (SEIM). 4-8-w-old callus transferred to mMS (liquid) at 100 rpm (suspension cultures). MS + 1 mg/l BA + 1 mg/l IAA + 5 mg/l hyg (SEMM). ½MS + 1 mg/l BA + 0.1 mg/l GA_3 (SIM). WB + 0.1 % AC (plantlet development). pH 5.7. 3 % sucrose	16-h PP. Light source NR. 45 µmol m^{-2} s^{-1}. 25 ± 2 °C	Embryogenic suspension cultures genetically transformed with *Agrobacterium tumefaciens* harbouring pCAMBIA 1301 (2008) or pD35SHER (2010) (see text for details). Shoots formed in 10–15 % of transformed tissues, with 100 % conversion to plantlets	Shekhawat et al. (2008, 2010)
S. album	MS + 4 µM BA (SGM). pH 5.8. 3 % sucrose. 0.65 % agar	16-h PP. CWFT. 55 µmol m^{-2} s^{-1}. 25 ± 2 °C	80.7 % of seeds germinated with GA_3 (pre)-treatment vs 46 % in control. Polyembryony observed in 2–3 % of seeds. Plantlets could be maintained for about 2 years in the absence of a host after acclimatization of 1-months-old seedlings in soil	Nikam and Barmukh (2009)
S. album	MS + 1 mg/l 6-BA, MS + 1 mg/l 2,4-D or MS + GA_3 (SGM). pH NR, carbohydrate, gelling agent NR	Darkness for SGM. Transfer to 16-h PP after germination. CWFT. 40 µmol m^{-2} s^{-1}. 25 ± 1 °C	Mature seeds could germinate on MS + GA_3 after 7–10 days culture and seedling induction was 82.5 % after 45 days of culture	Mo et al. (2010)
S. album	MS + 1 mg/l BA + 0.5 mg/l GA_3 (SGM; 2011, 2012). MS + 1 mg/l 2iP (SIM, SMM; 2011). MS + 1 mg/l TDZ (SIM; 2012). CIM + 10 % CM (SEM; 2011, 2012). ½MS + 0.5 mg/l IBA + 0.25 mg/l NAA (RIM; 2011). ½MS + 0.5 mg/l IAA (RIM; 2012). pH 5.6. 3 % sucrose. 0.9 % agar	16-h PP. CWFT. 40 µmol m^{-2} s^{-1}. 25 ± 1 °C. 55–60 % RH	72 % SGM. 41.0 shoots/explant after 45 days (2011) or 52.3 shoots/explant (2012). 4.2 roots/shoot after 6 weeks (2011) or 6 roots/shoot after 40 days (2012). 70 % survival of acclimatized plantlets in red soil + vermiculite + FYM (1:1:1) at 60–70 % RH (other conditions NR) and watered with dilute MS (2011, 2012)	Janarthanam and Sumathi (2011); Janarthanam et al. (2012)

Table 4 continued

Studied sandalwood[a]	Culture medium, PGRs, additives, subcultures[b]	Culture conditions[c]	Experimental outcome, maximum productivity, acclimatization and variation	References
S. album	MS + 4.44 µM BA + 2.69 µM NAA (SGM). MS + 13.5 µM 2,4-D (SEIM). MS + 2.22 µM BA + 1.44 µM GA_3 (SEM). ½MS + 2.46 µM IBA (RIM). pH 5.6. 3 % sucrose. 0.9 % agar	16-h PP. CWFT. 2000 lux. 25 ± 2 °C	80 % SG. 60 % of internodes showed an embryogenic response on SEIM within 4–6 weeks. 65 % shoot elongation after 25 days. 60 % of shoots rooted in RIM. 60 % survival of acclimatized plantlets in sterile soil + sand + vermiculite (1:1:1)	Revathy and Arumugam (2011)[e]
S. album, *S. yasi*, R1 hybrids	PGR-free MS (SIM). MS + 2 µM BA + 0.02 µM NAA (RIM). pH 5.7. 2 % sucrose. 0.7 % agar	16-h PP. CWFT. 30 µmol m^{-2} s^{-1}. 25 °C	Shoot formation in 8 m. 13.5 % survival after shoot formation for *S. yasi* (results for *S. album* and R1 hybrids NR). 19.1 % survival after root formation for *S. album* (results for *S. yasi* and R1 hybrids NR)	Baiculacula (2012)
S. album	MS + 1 mg/l 2,4-D + 0.5 mg/l TDZ (direct and indirect SEIM). MS + 2 mg/l 2,4-D + 0.5 mg/l TDZ (indirect SIM). MS + 2 mg/l 2,4-D + 0.5 mg/l NAA (direct SIM; plantlet regeneration via direct organogenesis). MS + 2 mg/l TDZ + 1.0 mg/l GA_3 (plantlet regeneration via somatic embryogenesis). MS + 1 mg/l TDZ + 0.5 mg/l GA_3 + 0.5 mg/l NAA (plantlet regeneration via indirect organogenesis). pH 5.8. 3 % sucrose. 0.75 % agar	Darkness for 1 w. 16-h (CIM, SIM) or 12-h (plantlets) PP. CWFT. LI and source NR. 25 ± 2 °C	Direct somatic embryogenesis (11.44 %), indirect somatic embryogenesis (54.23 %): 160.08 SEs/explant; indirect organogenesis (20.38 %); direct organogenesis (9.48 %); regeneration of plantlets via direct organogenesis (36.69 %); plant regeneration via somatic embryogenesis (163.63 %) or 141.25 % via indirect organogenesis. Roots could not be induced from any medium. Acclimatized plantlets in sand + soil + FYM (sterilized mixture; 1:1:1), but survival not quantified. Protocol very complex and values >100 % difficult to interpret	Bele et al. (2012)[e]
S. album	B_5 + 3 % sucrose. 0.78 % Bacto agar (SGM). MS + 0.5 µM 2,4-D + 10 µM Kin (CIM). B_5 + 0.5 µM 2,4-D + 10 µM Kin (CMM). MS + 2.5 µM Kin (SIM from green callus). pH 5.7. 3 % sucrose. 0.78 % Bacto agar	16-h PP. CWFT + purple photosynthetic lamps. 6000 lux. 27 °C	96 % SG in vitro. 1 % infection. 2 % polyembryony (discarded). No in vitro rooting possible from callus-derived shoots. Seedlings planted with grafted 2-year-old *Citrus* as pot host. GC–MS used to analyze the composition of callus following extraction with pentane	Crovadore et al. (2012)
S. album	WPM + 990 mg/l K_2SO_4 + 100 mg/l *myo*-inositol + 0.4 mg/l TDZ (CIM). WPM + 2.5 mg/l BA + 0.4 mg/l NAA (SIM). WPM + 1.5 mg/l IBA (RIM). pH 5.8. 3 % sucrose. 0.8 % agar	16-h PP. CWFT. 36 µmol m^{-2} s^{-1}. 25 ± 2 °C. 40–60 % RH	2013: 100 % of explants formed callus; 24.6 shoot buds/callus; 20.7 shoots/explant; 91.7 % of shoots rooted. 2015: 100 % of explants formed callus; 16 shoot buds/callus; 82.37 % of shoots rooted. >90 % of plantlets acclimatized in sterile soil and coco-peat (1:1) (2013) or 85 % of plantlets acclimatized in sterile soil, sand and coco-peat (1:1:1) (2015) survived after 4–5 weeks	Singh et al. (2013, 2015)

Table 4 continued

Studied sandalwood[a]	Culture medium, PGRs, additives, subcultures[b]	Culture conditions[c]	Experimental outcome, maximum productivity, acclimatization and variation	References
S. album	MS + 2.5 mg/l 2,4-D + 3 mg/l Kn (CIM). MS + 0.5 mg/l BA + 1 mg/l IAA + 0.5 mg/l Kn (SEIM). MS + 2 mg/l GA_3 (SGM). MS + 0.4 mg/l BA + 0.2 mg/l IAA (plantlet development medium). pH 5.8. 3 % sucrose. 0.78 % jelly moss	25 ± 1 °C, LI + source NR Dark for callus and SE induction. PP = 16 h for SE germination and plant development	Callus induction observed with 8 weeks and SEs within 2 weeks. About 58 % of SEs germinated within 2 weeks. About 76 % of plantlets produced with healthy shoots and roots. Acclimatization NR	Peeris and Senarath (2015)

2,4-D, 2,4-dichlorophenoxyacetic acid, *2iP* N^6-(2-isopentenyl) adenine, *AA* ascorbic acid, *ABA* abscisic acid, *AdS* adenine sulfate, *B_5 medium* or Gamborg medium (Gamborg et al. 1968), *BA* N^6-benzyladenine (BA is used throughout even though BAP (6-benzylamino purine) may have been used in the original, according to Teixeira da Silva, 2012a, *BM* basal medium (in mg/l: $KINO_3$ (1900), NH_4NO_3 (1650) $CaC1_2{\cdot}2H_2O$ (440), $MgSO_4{\cdot}7H_2O$ (370), KH_2PO_4 (170), $MnSO_4{\cdot}4H_2O$ (25), H_3BO_3 (10), $ZnSO_4{\cdot}7H_2O$ (13.9), Na_2EDTA (18.6), *myo*-inositol (100), nicotinic acid (5), folic acid (5), glycine (2), pyridoxine–HCl (0.5), thiamine-HCI (0.5), biotin (0.05), sucrose (20 g/l), Difco bacto agar (6 g/l) modified WB according to Rangaswamy (1961)); CA, citric acid; CH, casein hydrolysate; *CIM* callus induction medium, *CM* coconut milk, *CMM* callus multiplication medium, *CSC* cell suspension culture, *CWFT* white fluorescent tubes, *FYM* farmyard manure, *GA_3* gibberellic acid, *GC–MS* gas chromatography-mass spectrometry, *hyg* hygromycin, *IAA* indole-3-acetic acid, *IBA* indole-3-butyric acid, *Kin* kinetin (6-furfurylaminopurine), *LI* light intensity, *mBM* modified basal medium (BM), *MES* 2-(*N*-morpholino)ethane sulfonic acid, *MS* Murashige and Skoog (1962) medium, *mMS* modified MS, *mWM* modified White's basal medium (White 1963), *NAA* α-naphthaleneacetic acid, *NOA* napthoxy acetic acid; *NP* not performed, *NR* not reported in the study, *PCM* protoplast culture medium, *pCPA* para chlorophenoxyacetic acid, *PGR* plant growth regulator, *PP* photoperiod, *RH* relative humidity, *RIM* root induction medium, *rpm* revolutions per minute, *SD 8339* 6-benzyl-9-tetrahydropyran adenine, *SE* somatic embryo, *SEIM* somatic embryo induction medium, *SEMM* somatic embryo multiplication medium, *SEM* shoot elongation medium, *SGM* seed germination medium, *SIM* shoot induction medium, *SMM* shoot multiplication medium, *SW-1* sandalwood suspension culture-1, *SW-2* sandalwood suspension culture-2, *TDZ* thidiazuron (*N*-phenyl-*N*′-1, 2,3-thiadiazol-5-ylurea), *TPM* tissue proliferation medium, *V47 medium* (3 mM MES + 0.5 mg/l 2,4-D + 0.5 mg/l BA, Binding 1974), *vvm* volume of air per unit medium per unit time, *WB* White's basal medium (White 1963), *WPM* woody plant medium (Lloyd and McCown 1980), *YE* yeast extract, *Zea* zeatin

[b] Even though calli was used in the original, the term callus has been used here based on recommendation of Teixeira da Silva 2012b

[c] The original light intensity reported in each study has been represented since the conversion of lux to μmol m^{-2} s^{-1} is different for different illumination (main ones represented): for fluorescent lamps, 1 μmol m^{-2} s^{-1} = 80 lux; the sun, 1 μmol m^{-2} s^{-1} = 55.6 lux; high-voltage sodium lamp, 1 μmol m^{-2} s^{-1} = 71.4 lux (Thimijan and Heins 1983)

[d] Most likely GA_3

[e] Claims of somatic embryogenesis without sufficient proof (cytological, histological, genetic), i.e., only photos of macromorphology[a]Genera: *S.* = *Santalum*

greater detail in Tables 3 and 4. The most recent reviews on sandalwood tissue culture and related biotechnologies were published by Rao and Bapat (1992), (1993), (1995), Bapat and Rao (1992a), and Bapat (1993)

Perspectives and culture establishment

Most in vitro studies have been conducted on *S. album* with only one report on *S. spicatum* (Tables 3, 4). *In vitro* tissue culture and micropropagation are popular methods for the large-scale propagation and improvement of existing plant genotypes, serving as the basal method for genetic transformation experiments, often cutting the time to obtain novel germplasm through conventional breeding. By providing a sterile culture environment, in vitro tissue culture also allows for developmental events to be studied, more so when thin cell layers are used (Teixeira da Silva and Dobránszki 2013), and for the production of in vitro flowers (Teixeira da Silva et al. 2014), which can serve as the source of disinfected floral tissues for either in vitro breeding experiments or more specialized in vitro techniques such as anther or ovary culture. The latter two techniques have not yet been applied to any *Santalum* species. The establishment of an in vitro propagation protocol traditionally requires several stages: culture initiation (including the appropriate choice of explant, surface sterilization, culture conditions and medium composition), multiplication, rooting (in vitro and *ex vitro*), acclimatization, and field establishment. These are outlined next for *Santalum* spp.

Choice of explant and surface sterilization

The choice of an explant depends primarily on the desired objective (e.g., shoot tips or nodal explants for the production of true-to-type clonal plants) or on the availability of healthy (disease-free) material. The age and physiological status of the mother plant need to be considered, such

Fig. 2 *In vitro* adventitious shoot propagation and root formation in *Santalum album*. **a** Adventitious shoots were induced on MS medium supplemented with 5.0 μM BA and 0.5 μM NAA. **b** Adventitious shoots were propagated and subcultured on MS medium supplemented with 5.0 μM BA and 5.0 μM IBA. **c** Root formation on rooting medium supplemented with 250 μM IBA. Unpublished figure/photos (Guohua Ma)

as actively growing vs dormant shoots, which often depends on seasonal availability. For the micropropagation of sandalwood, various explants have been used. Details about explant source, the type of explant used, and their size are described in Table 3. In general, the micropropagation of any plant species employs explants with a predetermined meristem such as a node or a shoot tip, either from mature trees or from in vitro or ex vitro germinated seedlings; other explants such as internodes, stem segments, or leaves of leaf disks are generally utilized to induce adventitious shoots or somatic embryos. In sandalwood, the explants used encompassed nodes and shoot tips from mature trees or seedlings (Rao et al. 1984; Muralidharan 1997; Das et al. 1998; Rugkhla and Jones 1998; Radhakrishnan et al. 2001; Ilah et al. 2002; Primawati 2006; Sanjaya et al. 2006a, b; Revathy and Arumugam 2011; Peeris and Senarath 2015; Singh et al. 2015), zygotic embryos and seed endosperm (Rangaswamy and Rao 1963; Rao 1965; Rao and Rangaswamy 1971; Rao and Raghava Ram 1983; Sankara Rao et al. 1996; Rai and McComb 1997; Shiri and Rao 1998; Anil et al. 2000; Anil and Rao 2000; Rai and McComb 2002; Mo et al. 2008), mature and immature seeds as well as seedling-derived explants such as internodes, hypocotyls, leaves, and stem segments (Rao and Bapat 1978; Bapat and Rao 1979, 1984; Lakshmi Sita et al. 1980a; Bapat et al. 1985; Das et al. 1999, 2001; Sanjaya and Rai 2003; Mujib 2005; Mo et al. 2008, 2010; Shekhawat et al. 2008; Nikam and Barmukh 2009; Shekhawat et al. 2010; Revathy and Arumugam 2011; Janarthanam and Sumathi 2011; Bele et al. 2012; Crovadore et al. 2012; Janarthanam et al. 2012), and explants such as leaves, stem segments, and internodes from mature trees (Lakshmi Sita et al. 1979; 1980b; Lakshmi Sita and Shobha Rani 1983; Rao and Raghava Ram 1983; Ozias-Akins et al. 1985; Rao and Ozias-Akins 1985; Lakshmi Sita 1986; Bapat and Rao 1988, 1992b, 1999; Bapat et al. 1996; Ma et al. 2008; Shekhawat et al. 2008; Singh et al. 2013). In rare cases (Bhaskar and Rao 1983), in vitro-raised shoots derived from callus were used explants although details about callus induction were not reported.

Surface sterilization, an essential step for the initiation of an aseptic culture, varies depending on the explant type and source (Table 3). In sandalwood, surface-sterilized fruits can be used for aseptic seed germination and to isolate endosperm (Rao and Bapat 1978, 1979; Bapat et al. 1985; Das et al. 1999; Ilah et al. 2002; Mujib 2005; Crovadore et al. 2012). Once an aseptic seedling has germinated, it can be used as a source of explants that does not require further surface sterilization (Rangaswamy and Rao 1963; Rao 1965; Rao and Rangaswamy 1971, 1999; Anil et al. 2000; Anil and Rao 2000). For surface sterilization, $HgCl_2$ in concentrations ranging from 0.05 to 0.5 % (w/v) are most frequently used, irrespective of the explant (Table 3). Even though the choice of sterilant, its concentration, treatment time and rinses are all essential aspects of a surface sterilization protocol (Teixeira da Silva et al. 2015), such basic information is frequently missing from many protocols, as is a description of the efficiency of the sterilization protocol and the quantification of infection (Table 3).

Culture conditions

Specific and tested culture conditions are required to initiate a plant tissue culture because photoperiod, light intensity, light source, and temperature play important roles in the successful establishment of an in vitro culture. The most commonly used conditions in the tissue culture of *S. album* were 16-h photoperiod and temperatures between 24 and 28 °C (Table 4), although some protocols used a 12-h photoperiod (Lakshmi Sita et al. 1979, 1980a, b; Sanjaya et al. 2006a, b) or very rarely a 14-h photoperiod (Shiri and Rao 1998). Rao et al. (1984) used a 72-h dark treatment for root induction. Optimal (recommended) in vitro regeneration protocols for *S. album* would be Singh et al. (2013, 2015) for callus induction, Rugkhla and Jones (1998) for somatic embryogenesis, and Sanjaya et al. (2006a, b) for direct shoot induction from leaf explants.

Medium composition

Medium composition includes the type of basal medium used or the composition and concentration of macro- and micronutrients, carbon source, gelling agent (type and concentration) or liquid culture, plant growth regulators (PGRs), and additives. Mostly Murashige and Skoog (1962) (MS) basal medium was used for *S. album* culture initiation, multiplication and rooting (Table 4). Only one study (Singh et al. 2013) used woody plant medium (WPM) (Lloyd and McCown 1980). Singh et al. (2013) used WPM with 990 mg/L K_2SO_4 to induce callus from leaves of *S. album* while WPM with PGRs was used to induce shoots and roots (Table 4). Crovadore et al. (2012) used B5 medium (Gamborg et al. 1968) for in vitro seed germination, while MS medium was used for callus culture, shoot induction, and rooting. In general, 3 % sucrose was used as the preferred carbon source, but 4–5 % sucrose was also reported in a few cases (Table 4). In most studies, semisolid medium was used and gelled with agar (Table 4), although Laxmi Sita et al. (1980a, b) used liquid culture medium for *S. album* somatic embryogenesis. Adventitious *S. album* shoots can be induced on MS medium supplemented with 5.0 µM BA and 0.5 µM NAA, subcultured on MS medium supplemented with 5.0 µM BA and 5.0 µM IBA, and rooted in the presence of 250 µM IBA (Fig. 2). Optimal basal medium for *S. album* would be WPM

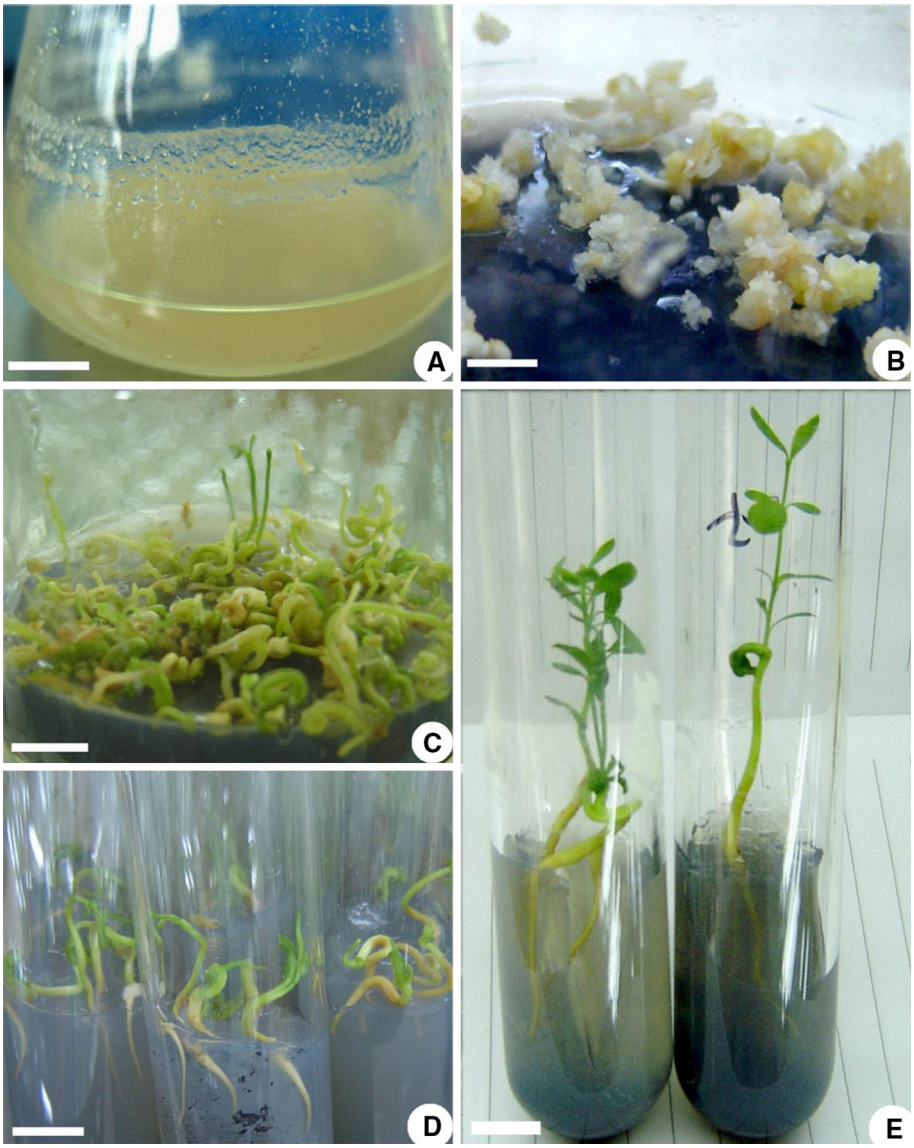

Fig. 3 Callus suspension, induced somatic embryogenesis, and plant regeneration in *Santalum album*. **a** Callus suspension in a flask in MS liquid medium supplemented with 4.5 µM 2,4-D. **b** Suspension cells transformed into embryogenic callus on solid MS medium supplemented with 5.0 µM TDZ and 0.5 µM IBA after 1 month. **c** Somatic embryos induced on MS induction medium supplemented with 5.0 µM TDZ and 0.5 µM IBA. **d** Somatic embryos germinated on 1/4 MS medium supplemented with 0.3 % activated charcoal and free of sucrose. **e** Plantlets regenerated from germinated somatic embryos on 1/4 MS medium supplemented with 0.3 % activated charcoal and free of sucrose. Unpublished figure/photos (Guohua Ma)

supplemented with 0.4 mg/l TDZ for callus induction (Singh et al. 2013, 2015), or MS supplemented with 5 µM BA for the induction of somatic embryos (Rugkhla and Jones 1998) or 0.53 µM NAA and 11.09 µM BA for direct shoot induction from leaf-derived explants (Sanjaya et al. 2006a, b).

Somatic embryogenesis

Somatic embryogenesis, an important in vitro plant regeneration pathway, is utilized for large-scale propagation and has various applications in cryoconservation, synthetic seed production, and as a source of protoplasts. A total of 33 in vitro *Santalum* propagation studies have claimed somatic embryogenesis (Rao and Rangaswamy 1971; Bapat and Rao 1979; Lakshmi Sita et al. 1979, 1980a, b; Rao and Raghava Ram 1983; Rao et al. 1984; Bapat et al. 1985; Ozias-Akins et al. 1985; Rao and Ozias-Akins 1985; Lakshmi Sita 1986; Bapat and Rao 1988, 1992; Bapat et al. 1990, 1996; Sankara Rao et al. 1996; Rai and McComb 1997; Das et al. 1998, 1999; Shiri and Rao 1998; Rugkhla and Jones 1998; Anil and Rao 2000; Das et al. 2001; Ilah et al. 2002; Rai and McComb 2002; Mo et al. 2008; Shekhawat et al. 2008, 2010; Revathy and Arumugam 2011; Bele et al. 2012; Singh et al. 2013, 2015; Peeris and Senarath 2015). Details about culture conditions and media composition to induce somatic embryogenesis are provided in Table 4. Despite these prolific reports, mainly for *S. album*, many have not been supported by very strong, or convincing, proof, such as histology, cytology, flow cytometry, or molecular markers.

Anil and Rao (2000) claimed that a Ca^{2+}-mediated signaling pathway may be involved in somatic embryogenesis after callus induced in the presence of 2,4-D took up four-fold levels of labeled Ca^{2+} resulting in the formation of pro-embryogenic cell masses. Spherical organelles in the endosperm are oil bodies in which calcium-dependent protein kinase (CDPK) (first purified in somatic embryos by Anil and Rao (2001), and termed swCDPKs) is expressed during seed development (Anil et al. 2003). As a result of the action of CDPK, the existence of these oil bodies and the Ca^{2+}-mediated signaling pathway, as much as 30 % of the dry weight of the endosperm was made up of oil (Anil et al. 2003). Earlier studies by this group (Anil et al. 2000) indicated that CDPK could not be detected in somatic embryos, or in the soluble proteins of shoots and flowers, but only in zygotic embryos, seedlings, and endosperm. *S. album* callus suspension that develops in MS liquid medium supplemented with 4.5 µM 2,4-D can be induced to form embryogenic callus on solid MS medium supplemented with 5.0 µM TDZ and 0.5 µM IBA, while somatic embryos form on MS medium supplemented with 5.0 µM TDZ and 0.5 µM IBA (Fig. 3).

Protoplasts

There are only four studies available in which protoplast culture was used for the regeneration of plants. Laxmi Sita and Sobha Rani (1983) isolated protoplasts from young leaves of mature *S. album* trees. In their protocol, leaves were incubated in 2 % cellulase R10, 0.5 % macerozyme, 0.5 % pectinase, and 1 % hemicellulase in cell protoplast washing (CPW) salts with 10 % mannitol at pH 5.6, incubated for 16 h at 25 °C with shaking. Protoplasts could be isolated by using only 1 % cellulase R10 and 0.5 % pectinase in V47 medium (Binding 1974). Leaves and callus yielded 2×10^5 and 3×10^6 protoplasts/ml, respectively. Protoplasts formed cellular colonies in 6 weeks after culture in liquid MS medium containing 2 mg/l 2,4-D, 0.2 mg/L BA and 10 % mannitol. The regeneration of organs or plantlets was not reported. Also in *S. album*, Bapat et al. (1985) used 1 % cellulase R10, 0.5 % macerozyme, and 0.5 M sorbitol or mannitol to isolate protoplasts from stem callus, 2 % cellulase R10, 1 % pectinase, 1 % hemicellulase, 0.9 % $CaCl_2 \cdot 2H_2O$, and 0.55 M sorbitol for hypocotyl callus and 2 % cellulase R10, 1 % macerozyme, 1 % hemicellulase and 0.8 M sorbitol for leaf mesophyll, all in V47 medium. The highest yield was from stem callus (8.73×10^6), and the authors claimed the production of somatic embryos and the subsequent development into plantlets. Ozias-Akins et al. (1985) also claimed to derive somatic embryos from callus induced from protoplasts derived from shoot segments using 1 % cellulase, 1 % macerozyme, 0.5 % driselase, and 0.55 M sorbitol. That study appears to have been a preamble for the more comprehensively reported study by Rao and Ozias-Akins (1985) in which the authors reported the same ideal enzyme cocktail for protoplast isolation from embryogenic cell suspension cultures derived from shoot segments of a 20-year-old *S.album* tree.

Genetic transformation

There are only three reports on the genetic transformation of sandalwood, all three targeting *S. album* and using *Agrobacterium tumefaciens*-mediated gene transfer. Shiri and Rao (1998) used LBA4404/pKIWI105 to introduce *gusA* and *nptII* genes into somatic embryos, confirming integration using a range of biochemical assays and molecular tools [GUS histochemical staining, NPTII expression assay, PCR, Southern blot, dot blot (equivalent to Northern blot)]. Disarmed *A. tumefaciens* strain EHA105 (Hood et al. 1993) harboring the pCAMBIA 1301 binary vector carrying the *gusA* gene driven by single CaMV 35S promoter and an *hptII* gene driven by a double-enhanced 35S promoter was used to transform embryogenic *S. album* callus (Shekhawat et al. 2008). Gene integration was confirmed by PCR, RT-PCR and Southern blot analysis, and GUS activity was shown to be stable over 7 months of culture. In an ensuing study, Shekhawat et al. (2010) transformed embryogenic cell suspension cultures—also with EHA105—with a hepatitis B small surface antigen (HBsAg) gene, encoding for a pharmaceutically important recombinant protein. Using electroporation and selection on kanamycin-supplemented medium, the authors confirmed transgene expression using RT-PCR, Western blot analysis, and ELISA. Supplementing medium with 30 mM trehalose almost doubled the level of HBsAg expressed. Genetic transformation is thus weakly explored in sandalwood species. However, the introduction of biotic (diseases, pests, viruses) and abiotic (drought, cold, frost, salinity) resistance through transgenic means would widen the possible niches where sandalwood could be cultivated, taking advantage of usually hostile conditions to harvest sandalwood products.

Conclusions and future perspectives

Sandalwood from several *Santalum* species is a commercially important forest product that has been traded for many centuries. International trade has been based on the harvest of wild stands, resulting in excessive exploitation and severe reductions in abundance and biodiversity across most species. This has led to sustained price rises for sandalwood products and increasing interest in sandalwood cultivation, both as an industrial crop and on a smaller

scale within agroforestry systems. Successful cultivation of sandalwood will depend on a clear understanding of its basic biology and propagation, details of which have been examined in depth in this review. The hemi-parasitic nature of sandalwood necessitates the planting of host plants to support its growth. While this makes cultivation of sandalwood more complex relative to other forestry species, many suitable species have been recorded in the literature to support sandalwood growth during the three main stages of its rotation (pot, intermediate, and final hosts). Sandalwood can potentially be grown across a range of environments provided locally adapted suitable host species are used from the nursery phase until harvest. It is evident that *Santalum* spp. preferentially form haustorial connections with N_2-fixing legumes (Table 2) and source significant N and C from these hosts. The breeding system can be described as incompletely outbreeding, with variation in the level of self-compatibility recorded between families and individuals. The capacity for self-fertilization within the genus is likely to have contributed to its capacity to colonize new territory/islands after long-distance seed dispersal by birds. No clear reproductive barriers exist between four commercial tropical species, and it may be possible that the capacity for hybridization between species is widespread in this genus. This feature of the breeding system can facilitate introgression of traits between species and development of hybrids. Introduction of exotic sandalwood species within the natural range of a compatible species will likely result in uncontrolled gene flow between them and modify the genetic structure and diversity of local species. The judicious application of biotechnology and cultivation may provide a viable alternative to extractive exploitation, leading to survival and proliferation of important members of the *Santalum* genus. This review highlights the successes and failures within the fields of plant tissue culture, as a means of mass propagating valuable germplasm. The ability to induce somatic embryos would allow synthetic seeds to be produced, aiding further germplasm storage, as cryopreservation units, and standardization (Sharma et al. 2013). Transgenic strategies, and genomic and transcriptomic analyses would allow for genes encoding for more rapid growth or for resistance to pests and diseases, such as spike disease, or to abiotic stresses, to be inserted, thus producing more robust and faster-growing trees.

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Compliance with ethical standards

Conflict of interest The authors declare no conflicts of interest.

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